

RYDER. (J. A.)

EMBRYOLOGY





(From the American Naturalist, January, 1885.)

EMBRYOLOGY.¹

AN OUTLINE OF A THEORY OF THE DEVELOPMENT OF THE UNPAIRED FINS OF FISHES.²—The median fins of fishes normally present five well-marked conditions of structure which correspond inexactly to as many stages of development, which, in typi-

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cal fishes, succeed each other in the order of time. A sixth exceptional form is developed in consequence of an extensive degeneration of the chordal axis and hinder end of the urosome, unaccompanied by an upbending of the hinder end of the axis as in the case of the evolution of heterocercy. The most primæval stages, or those found to appear in the younger phases of the growth of fishes are somewhat approximated by the structure of the fins of some of the most ancient Devonian, Triassic and Jurassic forms and by such living forms as Chimæra, the Dipnoans and Leptocardians, but the parallelism of the development of the tail of young fishes with the successive modifications of caudal structure found in the forms of successive geological periods is not exact, as we shall presently show.

1. *Archicercy*.—The most primitive modification of the urosome is that which I will call *archicercal*, and which is without any median fin-folds whatsoever. While it is true that only a few degenerate or specialized forms of true fishes (Hippocampus, Nerophis) approximate such a condition, it must be admitted that the fins are acquired structures, and that the folds from which they are developed have been acquired in the course of the evolution of the ancestry of the fishes. When a young fish is developing in the egg its tail grows out at first as a blunt prolongation backwards, which is for a time wholly without fin-folds, cylindrical and vermiform in general appearance, with the muscular somites clearly marked.

The larva of *Branchiostoma* (Fig. 1) is at first without median



Fig. 1.

fin-folds, and that of *Petromyzon* seems to be without them during the very early stages, and while we must make due allowance in both these cases for the effects of degeneration, we may, I think it probable, look upon these types as possessing at one stage a typically archicercal and vermiform tail. The solitary Urochorda or Ascidians pass through an archicercal stage of development of the urosome. In the course of further development the Ascidians never seem to pass beyond what I have called the second or lophocercal stage when it is absorbed in the caducichordate forms, but persists in the same stage in the perennichordate Appendicularia.

The Elasmobranchs seem to pass through an archicercal stage while the Amphibians do not exhibit it in so pronounced a way, very soon becoming lophocercal, though the larva of *Dactylethra* has the anterior part of the urosome with high median fin-folds while the termination is somewhat like that of *Chimæra monstrosa* (Fig. 2), but tapers more and is typically archicercal (*teste*, W. K.

Parker). After the absorption of the lophocercal tail of anurous amphibian larvæ has been in progress for some time, it seems to

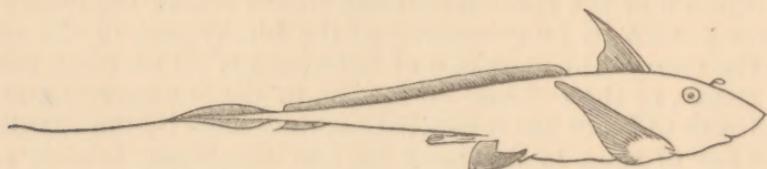
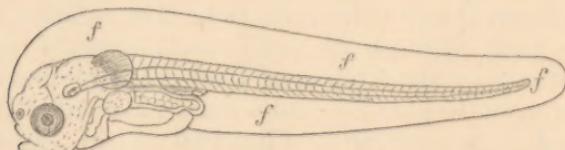


Fig. 2

tend to lose its median folds somewhat and revert to the archicerical condition. This is also the case with the young of most Urodela as they approach maturity.

2. *Lophocercy*.—The second stage of development of the median fin-system of Ichthyopsida is what I have called *lophocercal* = *protocercal*, Wyman; = *leptocardial*, A. Agassiz) when it consists of continuous folds (Amphibia, Elasmobranchs, Teleosts, etc.), or exceptionally of discontinuous folds (Siphostoma, Gambusia) which do not include permanent rays. The continuity of the median fin-fold in young fishes seems to depend somewhat upon the extent to which the permanent fins are approximated in the adult. Several forms amongst the Clupeoids develop an expanded eradiate caudal fold, with the chordal axis dividing it into equal moieties, which anticipates the form of the outwardly homocercal tail of the adult. At the close of the lophocercal condition the ray-bearing fishes at once diverge from the rest of the Chordata, and also the Urochorda, in that they develop *embryonic rays* in definite regions of the median fin-fold or continuously throughout its entire extent and which give rise to the rays of the distinct or continuous fins of the adult. The intervening parts of the fold in the first case atrophy (—local reversion to archicericy),

Fig. 3.



the materials for the formation of the rays being supplied partially by mesoblastic secretion, while the axial parts are of mesoblastic origin; the materials for the medulla of the rays being supplied by the outgrowth of mesoblast into the fold. The disposition of the materials for the development of the rays of the unpaired fins seems to be very decidedly under the control of heredity, which determines their permanent location or position in

the primitive fold, which may therefore be considered the matrix of the permanent fins.¹

In the formation of rays, their supports and musculature, there is clearly a close correspondence between the number of ray-bearing somites of the body and the one, two or three rays and supports which are developed to each segment, and this is manifested even when heterocercy and its accompanying degenerative processes manifest themselves in the caudal region of the most specialized forms.

3. *Diphycercy*.—The most archaic distribution of the median fin-rays is a continuous one, (as in Fig. 4), and is hypaxial from the vent to the end of the tail and then forward dorsally or epaxially; (*Cœlacanths*, *Placodermi*, *Dipnoids*, *Pleuracanthus*). Another archaic trait is the perfectly straight chorda or vertebral axis which extends without upward curvature in typically diphycercal forms to the end of the urosome. (An archaic trait which also marks a phase of the ontogeny of the Teleosts is the *Cœlacanthous*—hollow—condition of the bony portion of the spines and their supports.) Fishes with a long eel-like body have tended to remain diphycercal, while those whose bodies have been abbreviated have tended, with the exception of such forms as the *Heterosomata*, to develop discontinuous median fins which have very probably been derived in the first instance, from hypertrophied portions of a continuous series. This hypertrophy in some cases involved the whole series, e. g., *Platax*. The primæval pre-diphycercal or lophocercal condition is immediately followed by the next stage (Fig. 5) which, as we have seen, must have been developed from a more archaic condition or one of true diphycercy. There therefore occurs a more or less extensive elision or failure to develop a continuous series of rays when specialization sets in so as to produce a discontinuous system of median fins. Embryonic development therefore fails to exactly recapitulate the phases of evolution of the median fins. Even the embryonic rays which are of mesoblastic origin do not always form a continuous series. They are far more numerous than the permanent rays, and are characteristic of the diphycercal condition and represent a stage of fin development which may be called the *protopterygian*.

These views are fully substantiated by the development of the caudal skeleton of the eel, in which in spite of its slight hetero-

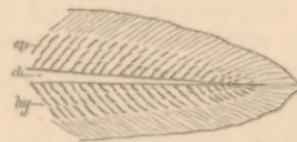


Fig. 4.



Fig. 5.

¹ Another article in the succeeding number will deal with the origin of the fin rays.

cery the diphycercal continuity of the fin-series has remained practically unimpaired, thus affording the necessary proof of the *serial homology* of the entire series of median fin-rays and their intermediary supports. (Previous authors failing to attack this part of the problem by the light of the ontogeny of a diphycercal eel-like type have missed the solution of one of the most important minor parts of a rational theory of the median fins, since it is otherwise impossible to prove such a homology in forms with atrophied intervals between the vertical fins.) The mesoblastic skeletogenous tract from which the median fin-rays and their supports are developed, is continuous in the median line of the urosome, above, below and almost over the end of the chorda in fish embryos ; such a continuity affords an explanation of why the median fin-rays form an uninterrupted series in cases of perfect diphycercy (Fig. 4), or where the archaic has not been replaced by a specialized mode of development, in the course of which discontinuity has arisen (Protopterus).

4. *Heterocercy*.—Heterocercy affects only the end of the chordal axis, which is bent upwards, and as a result of this it and the subsequently formed terminal vertebral segments are consolidated into a urostyle (many Teleostei), above and below which epaxial and hypaxial skeletal elements are formed, of which the former are, however, often aborted, and the latter widened as supports for the caudal system of rays.

This condition appears to result from two causes : (1) Great activity of growth in the terminal hypaxial part of the primitive caudal fin-fold in consequence of which the chorda is shoved upwards ; and (2) from the *actions* of the animal in using the resulting expanded, hypaxial, caudal, ray-bearing fold in swimming ; the strokes of the fin in action, owing to the resistance offered by the water, tend to throw up the somatic axis, just as an oar tends to be thrown upward in sculling.

Since the hypaxial fold may be developed at some distance from the end of the tail, in the more specialized forms (Lepidosteus, Fig. 6 ; Gasterosteus) a more or less extensively free portion

Fig. 6.

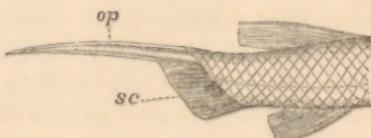


Fig. 7

of the lophocercal caudal axis is left to project (Fig. 7) during the growth of the true or secondary caudal, the rays of which are mostly hypaxial and serially homologous with those of the anal. The exserted part of the larval axis alluded to above, may be called the *opisthure*, in reference to its position in relation to

the permanent caudal. It subsequently degenerates, or it may persist as a prolongation of the chordal axis covered by integument, as in *Chimæra monstrosa* (Fig. 2) or, as in heterocercal *Amiurus* (Fig. 8), it may, at an early stage, have the chorda exserted beyond the last hypural cartilages and at some distance behind them have another hypaxial cartilage (*op*) developed, which may be called opisthural, as it probably represents the remnant of proximal hypural pieces, which were developed in some more primitive ancestral form in which diphycercy was more pronounced or even perfect. Where the caudal, ray-bearing fin-fold is developed nearer the end of the chordal axis (*Apeltes*, *Siphostoma*, *Gambusia*,) heterocercy is not

so pronounced, as the urostyle is shorter and only one or two of the terminal vertebræ are involved, whereas in other cases (*Salmo*, *Lepidosteus*) more terminal vertebræ may be implicated by degeneration. In archaic forms of heterocercy there may be epaxial rays and intermediary supports developed, while the hypaxial supports and rays extend to the end of the upwardly bent termination of the axial column (Fig. 5). This trait may possibly differentiate the archaic type of heterocercy (*Palæoniscus*, *Platysomus*, *Acipenser*, *Squali*) from the more recent or specialized form (*Amiurus*, Fig. 8) now prevalent amongst Teleosts, and which have for the most part a more or less well-developed urostyle, but with a very short or included opisthure (= dorsal lobe, A. Agassiz), and with the epaxial spines of the urostyle displaced, rudimentary or aborted. Outwardly homocercal Palæozoic fishes (*Dapedius*, *Pycnodus*,) probably had an opisthural filaments developed during their larval stages which subsequently became aborted, as in *Lepidosteus*, but in others (*Platysomus*, *Pygopterus*,) the terminal part of the chordal axis doubtless became segmented, the segments bearing hypaxial caudal rays and few or no epaxial ones, so that their opisthures were probably rudimentary or wanting.

It thus becomes evident that the development of modern Teleosts presents only a partial or inexact parallelism with that of the Palæozoic Rhomboganoidei, for few, if any, of these forms show the urostyle so distinctly developed or the hypural pieces so extensively coössified as in existing Teleostei, and we have also shown that there is no such thing even as an exact parallelism to be discovered between the development of the tail of the embryos of the latter and that of the embryos of an existing representative of Palæozoic forms, viz., *Lepidosteus* (Fig. 6). The Rhom-

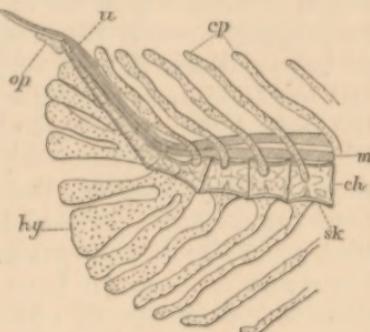


Fig. 8.

boganoidei, Cycloganoidei, Crossopterygia and Chondrostei show a more decided tendency towards the development of a dorsal and ventral, or, only a ventral series of caudal rays which extend to the end of the caudal axis, and thus trend more towards a diphycercal condition than the existing Teleostei, which may be said to be verging towards *hypocercy* when all of the caudal rays will be of hypaxial origin, with very often a rayless interval between the last hypaxial pieces and the end of the exserted urostyle (Fig. 8), the latter finally tending to become shorter and be aborted as in *Fistularia* and *Apeltes*. These are some of the marks of progress which distinguish the Teleosts and supplement the significant fact of their well-ossified skeleton. It is highly probable that we shall find no remains of the larvæ of Palæozoic fishes in the rocks, so that we have no means of contrasting their early phases with those of existing forms, but it is certain that none of the most simple forms of the Palæozoic fishes, in respect to their caudal skeletal structure, even approximate such a primitive condition as the lophocercal stage of modern forms; the only trait which they possess in common are the continuous median fins; in the first instance containing rays, in the latter case being without them. When we know the larvæ of *Ceratodus*, *Polypterus*, *Lepidosiren* and *Protopterus*, as well as we know that of *Lepidosteus* we may have a moderately comprehensive understanding of the main features of the development of Palæozoic fishes.

The evidence in favor of degeneration of portions of the caudal region of fishes is the existence of a permanent archicercal opisthure in *Chimæra monstrosa* and *Stylephorus chordatus*; the extensive development of a temporary opisthure in *Lepidosteus*; the concrescence of the hypural pieces; the ventrally diplacanthous and even triplacanthous caudal vertebræ (Fig. 8), or their coalesced representative, the urostyle; the existence of hypaxial opisthural elements; the abortion of the epaxial spines of the caudal vertebræ, and finally the abortion or extreme modification of the last muscular somites of the caudal region.

5. *Homocercy*.—This merely expresses the condition of epaxial and hypaxial symmetry presented by the fan-shaped caudal of Teleosts, and is the final term in the evolution of the growth of the rays of that fin, in consequence of which the archaic symmetry of perfect diphycercy becomes again restored, though the axial structure of the tail is heterocercal.

6. *Gephyrocercy*.—This type of tail appears to be normally met with in only two forms of Teleosts, viz., *Mola* and *Fierasfer*. The primitive opisthure or end of the urosome in these forms is apparently aborted, in the first, in the course of larval existence, in the other during post-larval life. As a result of this a hiatus is left between the epaxial and hypaxial rudiments of the median fins, and in the center of this hiatus the axial column ends

abruptly as if cut or bitten off, the hinder hypaxial and epaxial tissues concerned in the formation of rays and their supports are then approximated over the end of the aborted axis so as to form a continuous chain, and developed later than the other and more anterior median fin rays (Mola), and the interval so bridged by a secondary process of development leads to the formation of what we may call a gephyrocercal tail, in which the spinous axial apophyses of the caudal vertebrae, together with their centra, fail to develop, and the caudal rays rest either upon interspinous elements alone, or even these may be almost entirely aborted, as is the case for a time in the young stages of *Mola* "*Ostracion biops*" and "*Melacanthus*," both of which are evidently young, post-larval phases of that form.

The views here outlined rest partly upon facts of my own observation, but I must express my great indebtedness to the researches of L. and A. Agassiz, Vogt, Lotz, Balfour, Parker, Huxley and Kolliker, whose labors have enabled me to coördinate the facts and establish doctrines respecting the origin of the median fins, which are founded upon the theory of ontogeny.—*John A. Ryder. Nov. 3d, 1884.*

EXPLANATIONS OF FIGURES.

FIG. 1.—Larval Branchiostoma, (after Kowalevsky); almost perfectly archicercal.

FIG. 2.—*Ctenorhynchus*, with an archicercal opisthural filament, (after Agassiz).

FIG. 3.—Leptocephalous larva of the eel-fish, with continuous median fin-fold, *ffff*.

FIG. 4.—Ideal diphyerceral tail, nearly as in *Ceratodus* and *Protopterus*.

FIG. 5.—Ideal archicercal heterocercal tail, somewhat as found in sturgeons and sharks.

FIG. 6.—Heterocercal tail of larval *Lepidostomus* (after Balfour and Parker), showing epural and hypural pieces undeveloped at the end of the chorda.

FIG. 7.—Tail of a very young *Lepidostomus* (from the same source), showing the opisthure, *op*, above the secondary or true caudal, *sc*.

FIG. 8.—Caudal skeleton of a larval *Amiurus*, fifteen days old. *op*, opisthural; *hp*, hypural; *al* and *ep*, caudal cartilages; *u*, *u*, style; *m*, meillula spinalis; *ch*, chorda, invested by the skeletal tissue, *sk*, of the caudal vertebrae.

PHYSIOLOGY.¹

THE THERAPEUTIC EFFECTS OF OXYGEN AND OF OZONE.—It is a popular error that breathing pure oxygen would prove destructive to animal life by greatly accelerating combustion in the body as it does of the fuel of an ordinary fire. Filipow has lately submitted the question of the physiological action of oxygen and ozone to exact experiment on men and dogs; his results may be summed up as follows: 1. Breathing pure oxygen is followed by no effects which distinguish its action from that of pure atmospheric air, at least as regards pulse, respiration and body temperature. 2. In cases of poisoning with chloroform, alcohol, sulphuretted hydrogen or carbonic oxide, respiration of pure oxy-

¹ This department is edited by Professor HENRY SEWALL, of Ann Arbor, Mich.

gen offers no advantages over that of pure air. 3. Breathing in diluted ozone is without the narcotizing effects which some ascribe to it. 4. Respiration in concentrated ozone produces powerful irritation of the mucous membrane, and is therefore injurious. 5. There is no proof that ozone is taken into the blood through the lungs.—*Pflüger's Archiv.*, Bd. 34, S. 335.

THE PRESENCE, SOURCE AND SIGNIFICANCE OF SUGAR IN THE BLOOD.—Seegen publishes an interesting contribution to the much discussed question of the function of the liver in relation to carbohydrates. As is well known, Bernard and his followers regarded the liver as the sugar-making organ, and went so far as to maintain that the sugar thus formed was produced chiefly by the disruption of albuminous material. Pavy and others regard, in general, the liver as a sugar destroyer, by whose means the over-loading of the blood with absorbed carbohydrate is prevented. Seegen lends his support to the older school. He shows that sugar formation in the liver is a general physiological function shared by widely different groups of animals, herbivorous and carnivorous. He finds, moreover, that the liver, even when excised, has the power of producing sugar from peptone. Numerous researches on dogs gave the following principal results: 1. Sugar is a normal constituent of the blood, but varies in its proportions from 0.1 per cent to 0.15 per cent. 2. The sugar content of the blood in the right and left sides of the heart is the same. Differences between the proportion of sugar in arterial and venous blood are not constant but variable within narrow limits. The blood of the portal vein, however, nearly constantly contains less sugar than that of the carotid artery. 3. The blood which leaves the liver contains double the quantity of sugar held by that entering it. The mean of thirteen experiments gave for blood of the portal vein, sugar 0.119 per cent; for the hepatic vein, sugar 0.23 per cent. 4. The amount of sugar thus leaving the liver in the course of a day is very considerable. The amount produced by the dog's liver in twenty-four hours is calculated to vary from 200 to more than 400 grammes. 5. The blood-sugar is formed, at least in carnivorous animals, exclusively from albuminous bodies. 6. The sugar content of the blood rapidly diminishes when the liver is excluded. This sugar is used up in all the living tissues.—*Pflügers Archiv.*, Bd. 34, S. 388.

THE PREVENTION OF HYDROPHOBIA.—MM. Pasteur, Chamberland and Roux have made the following communication on the prophylaxis of rabies by inoculation with a modified virus. They find (1) that the virus transferred from the dog to the ape, and cultivated by propagation through several members of the latter order, becomes progressively feebler after each inoculation. After a certain period of such cultivation, if it be hypodermically administered to dogs, guinea-pigs or rabbits, or even by intracra-

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EMBRYOLOGY.¹

THE DEVELOPMENT OF THE RAYS OF OSSEOUS FISHES.²—Since the time when Vogt published his work on the development of the salmonoids, in 1842, it has been known that the earliest traces of rays to be noticed in the fin-folds of young fishes were fine, very numerous filaments, lying parallel to each other. Th. Lotz,³ in 1864, carried Vogt's observations farther, and thought he showed that by the coalescence of these filaments the rudiments of the permanent rays were laid down. Both A. Agassiz and myself have found these filaments in the embryo of numerous widely separated genera of teleosts; the former having also pointed out their existence in *Lepidosteus*. They also exist permanently in an almost unmodified form in the Dipnoans, as shown by the researches of Günther and others. Balfour and myself have found these filaments in all of the fin-folds of Elasmobranchs, though they seem to be wanting in the more fleshy pectoral of some of the Rays. They are present in the fin-folds of embryo sturgeons, and there probably give rise to the permanent

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² Abstract of portion of a paper on the theory of the fins, to be published, with plates, in the Proc. U. S. Nat. Museum.

³ Ueber die Schwanzwirbelsäule der Salmoniden, etc. Zeitsch. f. wiss. Zool., XIV, 2 Heft.

osseous rays as in Teleosts, but in very young Amphibians and Marsipobranchs they are absent, and in *Amphioxus* the development of the so-called rays at the bases of the vertical fins is so entirely different, according to Kowalevsky's account, that they are manifestly not homologous with the homogeneous embryonic radial filaments found in the fins of true fishes (Ganoids, Dipnoans, Teleosts, Elasmobranchs and Chimaeroids).

In all the forms so far made the subjects of observation, these embryonic filaments are much more numerous than the permanent rays, and appear clearly defined in sections between the mesoblast and epiblast which constitute the fin folds when the rays are being formed, these filaments then become covered externally by a more or less clearly defined layer of mesoblast about one cell deep, or, if they are not forced inwards in this way, they coalesce directly to form the basement membrane of the permanent rays. Usually, however, they are forced inward by the radial proliferation of the mesoblast spoken of above, and they then degenerate, their substance being apparently carried out to the surface of the mesoblastic core of the permanent rays by a process of metabolism to form the basement membrane of the latter which is crescentic in sections, and immediately overlaid externally by the integument. As this new formation takes place proximally it would appear that the primitive radial filaments had coalesced by their parallel sides distally, and fused into a continuous semi-tubular strip of basement membrane which maintains its more primitive fibrillated form distally or at the margin of the fin, thus giving rise to the dichotomous structure of the right and left halves of which a caudal fin-ray is almost always composed in osseous fishes.

The primitive radial fibers (embryonic fin-rays of A. Agassiz) appear first at about the end of the lophocerebral stage around the end of the tail and in the pectorals. In *Gadus* embryos, three weeks old, the first traces of these filaments appear at the end of the tail, in the vertical fold surrounding its extremity, as numerous elongated cells with fine protoplasmic prolongations extending in one direction toward the axis of the body and in the other away from it. These spindle cells are arranged like the filamentous rays which develop later, that is, their processes extend nearly parallel to the processes of those adjacent. These rudiments of the embryonic filaments bear a remarkable resemblance to cells found imbedded in the rays of *Ceratodus*, as figured by Günther in his memoir on that form. I will therefore call them *pterygoblasts*; their origin is mesoblastic and not epiblastic. They develop into the embryonic radial filaments, but the extent to which these are differentiated in the median fins of Teleosts is very variable. Amongst those forms which have continuous median fin-folds developed as well as a pre-anal fin-fold, *Salmo* is the only form known to me which has them developed through-

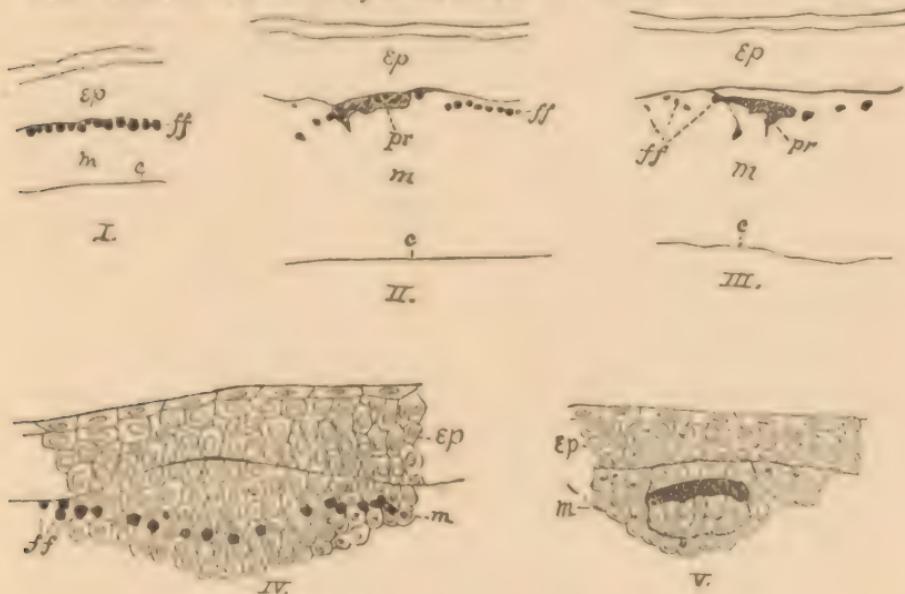
out the entire extent of those folds; *Alosa*, also a physostomous form, does not have them developed nearly so extensively at a corresponding period. In forms with discontinuous folds, as *Siphostoma*, for example, they are not very evident even at the time when the caudal rays are being formed, but aside from such exceptional forms they seem to be almost universally developed to some extent in the fin-folds of all truly fish-like forms except the lampreys and the lancelet.

In consequence of the striking resemblance which this stage of the development of the rays of the most specialized fishes bears to what has remained nearly permanent, with but comparatively little modification in the Chimæroids, Elasmobranchs, *Ceratodus* and *Protopterus*, I propose to call this the *protopterygian stage* of the development of the fin rays in the Teleostei. The primitive fibers in section are shown to be perfectly cylindrical and homogeneous, and so far as histological tests enable me to judge, are perfectly similar in composition to the homogeneous semitubular matrix derived from the former, in which ossification occurs to form the permanent rays. Active metabolism evidently occurs at the base of the fin-folds about the time the permanent rays are in process of development, for the reason that after the stratum of fibers becomes covered externally by mesoblast in this situation they rapidly atrophy leaving nothing but the semitubular rudiments of the permanent rays, crescentic in section, which now lie between the epiblast and mesoblast resting upon thickened tracts of the latter internally and which radiate toward the margin of the permanent caudal fin-fold; the proximal ends of these mesoblastic cores rest upon the distal end of the upturned chorda.

The segmentation of the permanent rays has not been traced, but this evidently occurs before ossification has gone very far, as it is manifested quite early in the caudal rays of certain types. It is doubtless due in part to the bendings which the rays suffer while in use. The rudiments of these rays are imperfectly tubular in all forms, spines also having such a form at first, though frequently these have an external layer added by coalescence with dermal plates or denticles.

The main conclusion, therefore, at which I have arrived in this investigation is the following: that it is the mesoblast which is involved in giving origin to the fibrous embryonic rays and that that layer also effects their transformation into the rudiments of the permanent rays, and not the epiderm or embryonic integument, as heretofore generally held by anatomists. The whole history of the fin-folds in fact favors such a conclusion, since the horny fibers develop between the corium and epidermis or embryonic skin, in the plane of the *protomorphic* line of Huxley. The fin-folds of embryo fishes, it should be borne in mind also, are at first wholly epidermic, the corium or true skin being only developed during the later-larval or post-larval life.

During my observations on the development of *Gadus*, made in 1881, I noticed a space which exists between the skin and muscle-plates (see Pl. x, Figs. 43 and 44, Contrib. Embryog. of Osseous Fishes), since then Carlo Emery¹ has published his observations founded on a study of transverse sections of the tails of



EXPLANATION OF FIGURES.

Portions of vertical transverse sections of the caudal fin of a salmon embryo, showing the development of the halves of the permanent rays of one side.

FIG. 1.—*ep*, deep and superficial layer of epiblast; *m*, mesoblast; *c*, center of mesoblastic tissue proliferated into the dermal tail fold; *ff*, filamentous embryonic fin rays cut transversely near the margin of the caudal fold.

“ 2.—From a section nearer the base of the fin to show the process of fusion of the primitive rays, *pr*. The other letters as before.

“ 3.—From a section in which the rudiment of the permanent ray, *pr*, is covered by mesoblast, the filamentous rays, *ff*, having been still more thickly enveloped on the outer or epiblastic side by the mesoblast than in Fig. 2. Traces of the presence of the filamentous embryonic rays can be seen in the substance of *pr* in this and the foregoing figure.

“ 4.—From a section through an outer caudal ray near its base, showing the fibers of enveloped externally by the mesoblastic core of the permanent ray, which forms a swelling which is cut across, on the top of which the first traces of the proximal end of the permanent ray appears.

“ 5.—Section through the basal part of a median ray, the primitive fibers in the vicinity having nearly disappeared, the ray itself again becoming covered externally by proliferated mesoblast. All of the figures enlarged 365 times, the cells being shown only in the two last.

embryos of *Fierasfer*, *Belone* and *Lophius*, in the early lophocerous stage. In these he finds a homogeneous secretion interposed between the muscle-plates and the epiblast, extending also into

¹Sulla esistenza del cosiddetto tessuto di secrezione nei vertebrati. Att. R. Accad. Sci., Torino, xviii, 1883.

the fin-folds, beside some scattering stellate mesoblastic cells which very possibly may be the pterygoblasts, which either themselves give rise to the embryonic rays or are indirectly concerned, together with the surrounding tissues, in pouring out such a homogeneous secretion. Such homogeneous substances I have found in other cavities in embryos, especially in the brain; in such cases I have been inclined to attribute their presence to the action of reagents, as extractive matters, as homogeneous, hardened acid-albumen, in short. The early advent of mesoblast into the fin-folds is at any rate a settled point, the stellate cells which wander outwards being mesenchymal, according to the terminology of the Hertwigs. In embryos of *Scomberomorus* I do not find the secretion noticed by Emery, homogeneous during the lophocercal condition, but loosely granular, more like the fine plasmic corpuscles found by me between the vitellus and zona radiata of the egg of *Amiurus*. At any rate I am not inclined to believe, after weighing the foregoing facts, that there is the slightest ground for the assumption that the fin-rays of fishes originate from the primary epiderm or larval integument, but that they arise from the mesoblast, as their position and first vascular supply would indicate. The distinction between the fin-rays as *exoskeletal*, from the other bones as *endoskeletal*, therefore breaks down on embryological grounds; for both are clearly of mesoblastic origin, as is further proven by the mode in which the insertions of the muscles which move the fin-rays originate.—John A. Ryder.

(From the *American Naturalist*, April, 1885.)

EMBRYOLOGY.¹

ON THE POSITION OF THE YOLK-BLASTOPORE AS DETERMINED BY THE SIZE OF THE VITELLUS.—This principle, which I have to some extent elaborated elsewhere (Cont. *Embryog. Oss. Fishes*, p. 114), in so far as it applies to the ova of bony fishes of different species, differing greatly in the dimensions of the vitellus, may be expanded so as to throw some additional light upon the growth and closure of the blastoderm of other groups of Vertebrata. In the paper cited I have shown that the position of the point of closure of the blastoderm in relation to the original position of the germinal disk in Teleostei is to a large extent determined by the size of the vitellus, and consequently also stands in an intimate relation to the variation of the area of the vitelline surface over which the blastodermic membrane must grow, that is to say, with the increase of the superficial area of the vitelline globe upon which the germinal disk is superimposed, and over which it spreads as the blastoderm, the position of the yolk blastopore must vary.

A yolk blastopore is met with only in such forms of ova in which there is a distinct, unsegmented or partially segmented vitellus developed. As a rule, it does not coincide with the position of either mouth or anus, but when such a coincidence does occur the yolk blastopore answers nearly or quite to the permanent anus of the Vertebrate embryo. In the Vertebrates the yolk blastopore is apt in most cases to close behind the position of the permanent anus; in large-yolked cephalopod ova it closes at the anterior or perhaps more properly on the ventral face of the yolk-sack, and seems to have no relation to either mouth or anus. This is also the case with the yolk blastopore of the embryo of Sauropsida in which it closes far behind the point where the true blastopore is formed.

In a large Teleostean ovum, as in those of the larger Salmonoids and marine catfishes, the embryo ceases to grow in length when it has extended itself over an arc of the yolk globe of, say, 90° to 125° ; in *Alosa*, an intermediate form, it extends its growth through an arc of 180° on the surface of the vitellus; in a third and still smaller type of ovum, that of *Carassius*, it may apparently grow to a greater length, and embrace an arc of 230° on the surface of the yolk sphere. In the first type that part of the rim of the blastoderm not yet incorporated into the body of the embryo and lying behind the latter may be drawn out into an oval, the anterior end of this oval area, over which the vitellus still remains uncovered, lying next the caudal extremity of the embryonic axis so far differentiated, as in *Tylosurus* and *Elacate*. This usually happens when the embryonic axis does not extend over a semicircumference of the vitellus, and when that half of

¹ Edited by JOHN A. RYER, Smithsonian Institution, Washington, D. C.

the blastoderm opposite the embryo must grow in width more rapidly than the embryonic half in which the embryonic shield is formed.

These different modes of the growth in length of the bodies of embryos of different species of osseous fishes may easily be verified by the observation of the progressive growth of the blastoderm of the living ova, and go far towards reconciling the differences of opinion which have been expressed by different observers as to the growth of the blastoderm over the yolk. It is at any rate evident that the manner in which this is accomplished in one form does not necessarily hold true of another.

It is very significant that two large-yolked types, viz.: the Sauropsida and Elasmobranchii should both have the embryo displaced in position in reference to the margin of the blastoderm. In the latter, the first traces of the embryo have the normal marginal position at the periphery of the blastoderm, but it is soon folded off, and before the yolk blastopore has closed, the latter finally closing a little way behind the stalk connecting the embryo and yolk sack. In the Sauropsida as held by Balfour, the primitive streak apparently represents the linear thickening between the lower vitelline stalk and the point where the blastoderm finally closed in the Elasmobranchii.

It is thus made evident that, whereas the embryonic axis in Teleostei, Chondrostei, Ganoidei, Petromyzon and Amphibia extends back to the point where the yolk blastopore closes, in Sauropsida and Elasmobranchii, the embryo is partially folded off, and the tail begins to bud out before the vitellus is included by the blastoderm, and while the end of the axis of the embryo is still remote from the opening of the yolk blastopore. This contrast between the two types, as will be evident to the thoughtful person, must be due to the great difference between the bulk of the yolks in the two cases. In the large-yolked forms if the embryonic axis were to continue to grow in length and extend quite to the point where the yolk blastopore closes, the body of the embryo would necessarily develop more somites than are present in the adult, so that growth in length of the embryonic axis ceases in the large-yolked forms far short of the point of closure of the blastoderm, covering perhaps only 30° of arc or less of the entire circumference of the vitelline globe. Such a small segment of the circumference of the vitelline sphere when contrasted with 90° - 125° , and on up to 180° to 230° , embraced by the primary embryonic axis in Anamniote forms, seems inconsiderable, but is really relatively as extensive as in the latter.

The germinal disk of Sauropsida is relatively much larger than that of Teleostei, so that proportionally it probably does not spread over a much larger vitelline surface in the first case than in the last in order to include the vitellus, but as the blastoderm spreads in either case, it must be obvious to any one conversant

with the mode in which the embryonic axis is formed during vertebrate development, that in the former growth in length of the axis would necessarily be completed before the blastoderm could spread over and include the yolk. Those forms of vertebrate embryos in which either the true or the yolk blastopore marks the end of the embryonic axis before the appearance of the tail bud might be called *teleporous*, while those in which there is no such coincidence, the yolk blastopore closing some distance behind or remotely away from the end of the embryonic axis, might be called, *ateleporous*. The first would include Amphibia, Petromyzon, Ganoidei, Chondrostei and Teleostei, the last, Elasmobranchs and Sauropsida. The ova of the two extremes of the vertebrate series Branchiostoma and Mammalia are yolkless, except those of Monotremata, which are probably ateleporous, simulating the Sauropsida in the general features of the development of the blastoderm and early phases of the embryo.

The band of tissue from the vitelline end of the umbilical stalk to the edge of the blastodermic rim in Elasmobranchii, and the primitive streak in Sauropsida and Mammalia are probably homologous structures. In the first instance it is formed by the concrescence of the margin of the blastoderm as it advances over the surface of the vitellus. In the Teleostei, Ganoidei¹ and Chondrostei it would seem that the whole of the margin of the blastoderm was used up by a process of concrescence to form the embryonic axis, whereas in the Elasmobranchii and Sauropsida there is a portion of the rim of the blastoderm remaining behind the embryo, which is not utilized in this way, but remains as the linear thickening of the former or as the primitive streak of the latter. While concrescence is not possible in the course of the development of the Sauropsida in the way in which it occurs in Ichthyopsida, it is known that the primitive streak is related posteriorly on either side to the *rand-wulst* or marginal thickening of the chick's blastoderm, a structure obviously homologous with the lower layer of the thickened margin of the blastoderm of the

¹ I regard the development of the germinal disk, embryonic axis and blastoderm of this type as being in no essential respect different from that of the Teleosts. The statements of Ballou and Parker, to the effect that the vitellus undergoes partial segmentation will probably be found to rest upon observations based upon material in which cracks were produced in the vitellus by reagents before the material reached their hands. The later stages show that I am right in this, the vitellus maintaining a relation to the body and intestine of the embryo quite like that observed in osseous fishes and totally unlike that noticed in the metoblastic ovum of Amphibians or Myzonts.

I am also unable to reconcile the figures given by Salensky and Professor W. K. Parker, of the fore part of the yolk sack of the embryos of Acipenser. If the figures of the latter are correct, which they probably are, the intestine does not enclose the vitellus as represented by Salensky, but passes as a closed tube over the top of the yolk just as in Teleostean embryos, the development of the sturgeons in this respect, it will be seen, differs but slightly from that of bony fishes, a conclusion which is also supported by the way in which the yolk disappears as well as by its position in relation to the body of the embryo.

fish embryo. It is therefore interesting to note that an actual con-crescence from behind forward of this *rand-wulst* or lower layer or a proliferation of cells from behind forwards would not be im-possible. The *inner mass* of cells of the Mammalian ovum while in the vesicular or blastodermic stage is evidently in part homologous with some part of the thickened rim of the blastoderm of lower forms.

It is also a matter of great interest in this connection to observe that in the Sauropsida the *rand-wulst* or germinal wall is not carried along with the extreme edge of the epiblastic stratum quite to the border of the blastoderm all round as in Ichthyop-sida. The epiblastic layer of the blastoderm in the Sauropsida rapidly extends beyond the lower layer or germinal wall, leaving it more or less remote from the outer margin of the germinal area. This peculiarity of development alone would be sufficient to cause the embryo to be formed away from the margin of the blastoderm in the Sauropsida, but even this I venture to suggest is to be explained by the increase in the size of the yolk of the ova of Sauropsida, the connecting link between the latter, and the teleporous Teleostean ovum being supplied by that of the Elasmobranchs, which probably represents at least one of the steps by which the evolution of the blastoderm of Sauropsida and Mammalia was attained, although it would obviously be incor-rect to assume that these stages of blastodermic evolution were indicative of a serial or successional affiliation through descent. It would probably be much more rational to regard the develop-ment of these differences as being in the main due to an increase in the volume of the yolk as urged by Balfour, and that the causes of variations in its development were therefore to some ex-tent mechanical in character.

The yolkless vesicular blastoderm of the higher Mammalia, or Eutheria, is obviously, as was supposed by Balfour, one which is to be regarded as having been derived from that of the Sauop-sida. But no yolk blastopore is ever formed in the mammalian blastodermic vesicle, unless the blastopore of Van Beneden can be regarded as such. The blastopore of Van Beneden is obviously not the true blastopore, and if it can be regarded as representing the yolk blastopore, which seems very probable, the *inner mass* of cells finally involuted on its closure or covered over by the epi-bolic growth of the epiblast, and from which mass the mesoblast and hypoblast are derived, that mass becomes homologous with the marginal lower layer or *rand-wulst* of such a type as the Teleostean ovum.

The degeneracy of the vitellus of the ovum of Mammalia may possibly be due to the development of the so-called *uterine milk* from the uterine glands by which the egg is nourished from with-out during a very early stage and before the development of the area vasculosa or the vessels of the allantois is accomplished.

Intracellular digestion and growth is probably accomplished by some of the cells of the epiblast of the blastodermic vesicle, which send out pseudopodal processes between the cells of the uterine epithelium, as described by Caldwell in the case of the blastoderm constituting the yolk bag of the embryos of certain Marsupialia. Viviparity has not affected the development of the vitellus in the Teleosts, Gumbusia, Zoarces and Embiotocidae, where fetal development is either intrafollicular or intraovarian. An albuminoid secretion is said by Blake to be found in the temporarily closed gravid ovaries of Embiotocoid fishes (*Journ. Anat. and Physiol.*, II, 280), and in this family as well as in some of the viviparous Elasmobranchs, it seems certain that the young developing viviparously are larger than can be accounted for by the size of the vitellus of the recently fertilized egg of the same species.

It therefore seems conceivable that the Mammalian vitellus, like the ambulatory, prehensile and other organs of parasitic organisms, may have been atrophied in consequence of the perfectly parasitic connection subsisting temporarily between the maternal organism and the embryo, as was supposed by Balfour.

—John A. Ryder.

DEVELOPMENT OF THE SPINES OF THE ANTERIOR DORSAL OF GASTEROSTEUS AND LOPIUS.—The important memoir of A. Agassiz before cited, shows that the spines of the anterior dorsal of the angler and stickle-back develop in distinct diverticula of the epiblast, a diverticulum being formed for each spine into which skeletogenous mesoblast is proliferated from its lower or proximal open end. These diverticula soon become free from the anterior end of the median dorsal fin-fold, the latter, in fact, seems to degenerate or be replaced by these diverticula, the first epiblastic diverticula to be developed are more or less translocated forwards from their original positions, so that in this way these dorsal spines are finally brought to rest on the roof of the skull of the adult, considerably in advance of the point where their development began on the nape of the embryo.

The formation of the singular dorsal appendage of the larva of *Fieraster* according to Emery⁴ is developed in a similar way as a dorsal epiblastic diverticulum, arising from the anterior end of the median dorsal fin-fold. The singular foliar appendages along its sides grow out secondarily. This transitory organ in *Fieraster* is, however, much more precociously and rapidly developed than the bony, anterior dorsal spines of *Lophius* and *Gasterosteus*; its supporting axis is evidently mesoblastic in origin as in the latter, but degenerates just about the time of the final metamorphosis of the animal into the adult condition.—John A. Ryder.

⁴ *Fieraster. Studi intorno alla sistematica, l'anatomia e la biologia delle specie Marin. di questo genere.* *Rivista Italiana dei Lavori Sci. 3^a, Mem. v. 1. di Ser. VII, 1880.*

(From the *American Naturalist*, May, 1885)

EMBRYOLOGY.¹

ON THE PROBABLE ORIGIN, HOMOLOGIES AND DEVELOPMENT OF THE FLUKES OF CETACEANS AND SIRENIANS.—We have seen that the development of the Physoclist fishes (AM. NATURALIST, 1885, pp. 315-317), shows that the translocation of the pelvic fins forward is accomplished in some forms in about twenty-four to forty-eight hours, to a position more or less in advance of the pectoral. If a limb fold can be translocated forwards in a vertebrate embryo from its archaic site, there is no reason to doubt that under certain conditions it might be translocated in the other direction or backwards. A process of translocation of the distal end of the pelvic limbs seems to have occurred in the cetaceans, as a consequence of which the pes has acquired a new position far to the rear of that which it occupies in normal mammals, and this seems to have been accompanied by processes of atrophy in some directions and hypertrophy in others.

The researches of Struthers, Flower, Reinhardt, Eschricht, Kaup, Lepsius, Howes and Wilder, leave no doubt as to the fact that the different rudimentary structures which these anatomists have detected, unequivocally point to the conclusion that, the cetaceans and sirenians have descended from Mammalia which possessed more or less perfectly developed ambulatory limbs, which fitted them at least for an amphibious or partially terrestrial existence. This conclusion is, I believe, generally accepted by recent authorities.

All recent writers, amongst which may be named Flower, Huxley, Owen, Claus and Parker, unequivocally declare that the hind-limbs of the whales and sirenians have been so completely suppressed, that no rudiments or vestiges of any kind have remained to indicate outwardly that these creatures ever possessed such appendages, the evidence that they did once possess hind-limbs resting for them rather upon the presence of a rudimentary pelvis with much reduced limb-bones in a few forms of Balaenoidæ and in Halitherium.

From this view the writer must dissent, having independently arrived at conclusions in reference to the homology of the flukes

¹ Edited by JOHN A. RYDER, Smithsonian Institution, Washington, D. C.

very similar to those published by Professor Gill¹ in 1882, who regards these characteristic structures as having been derived from greatly hypertrophied integuments of hind-limbs analogous to such as are developed, for instance, to the hind limbs of the eared seals, while the osseous elements have been inversely atrophied, pulled forwards, and reduced to supports for muscles connected with the organs of generation. It may, I think, be regarded as a fact that there is no evidence to show that development does not attempt to recapitulate in a disguised form, in the cetacean foetus, the outgrowth of the hind-limb as seen in a normal mammalian embryo.

In the mammal the pectoral limb is the first to appear, the pelvic appearing last. If the flukes be regarded as the outward vestiges of hind-limbs or pedes, then will the embryos of cetaceans and sirenians conform to this law presiding over the order of appearance of the limbs, which, so far as I am aware, is regnant without exception within the limits of the vertebrate class. The dorsal fin with which the flukes have so often been mistakenly compared, is not present in all cetaceans; is absent in all sirenians; is not constant in position in different genera of the former; is sometimes a mere carina, dorsal ridge or hump; its vascular and nerve supply is different from that of the flukes; it develops after the latter, showing that it is a later acquirement; it has absolutely no connection with muscles directly or indirectly by tendons as have the flukes, so that I regard the comparison of the dorsal fin, which is a mere dermal fold, with the flukes, as expressing a mistaken apprehension of anatomical homologies, and not justified in the face of the fact that the flukes are never absent, and always appear laterally or serially in the position of a hind limb-fold, though backwardly displaced. It must, however, be stated that I distinctly disavow the affirmation that the flukes are homologous with more than the pedes of normal forms. The older views which intimated that the flukes were the representatives of limbs or of feet, it is not worth while to discuss, as these writers did not possess the data upon which to base any reasons for their opinions, which seem to have been in the main intuitive.

The hypothesis which is offered to account for the flukes as the distal vestiges of limbs rests upon the following arguments:—1. The mode of outgrowth of the flukes in the embryo, prior to the dorsal fin, at the end of the sides of the tail, at first as a pair of low rounded lobes or folds of skin, containing mesoblast, which become gradually falcate, and which expand posteriorly so as to leave a notch over the end of the tail between their inner edges. The hind margin of the flukes answering to the terminal border of the pes or the ends of the suppressed toes or the integuments extending beyond them, and their anterior margin to the outer

¹ Scientific and popular views of nature contrasted. A lecture delivered in the National Museum, March 11th, 1882. Pp. 10-11. Washington, Judd & Detweiler.

digital border. 2. The existence of a small median papilla, according to Wilder, at the extreme end and under side of the tail of the fetus of the manate, representing apparently the last vestige of an exserted tail extending beyond and behind the fluke folds of this type, in which the flukes are in fact rudimentary. 3. The fact that the osseous elements of the limb have atrophied exactly in the reverse order in which they appear in the embryo, or from without inwards, that is, from behind forwards in cetaceans and sirenians, because in both, the hind-limbs have been rotated or extended permanently backwards distad of the knee joint. 4. The structure of the embryonic fluke-folds or diverticula filled with mesoblast comparable to that found in the limb-folds of other vertebrate embryos, these limb-buds representing structures which have survived translocation and made an attempt to imperfectly reconstitute the development of part of the limb.

The above headings present the embryological argument. The other data are anatomical and are mainly based on a comparison of the pinniped and cetacean types. Admitting that the cetaceans are descended from land forms, we would naturally look to types of amphibious habits and poorly adapted for progression upon land to furnish the first indications of modifications which have been carried to an extreme degree in the former. Traces of the beginnings of such modifications we actually find in pinnipeds.

In the pinnipeds, the hind limbs, from the knees, have been rotated backward and included by a continuation of the integument which invests the body together with the tail, leaving only the last two or three short caudal vertebrae exserted or projecting into a caudal integumentary pocket, lying between the distal parts of the backwardly extended limbs. This process of inclusion, if carried to an extreme stage, would finally cause the whole of the tail to be lost to sight outwardly, leaving only the metapodial and phalangeal parts free. As a result of this arrangement in the pinnipeds certain muscular insertions of the limb muscles have been moved backwards, and the hyposkeletal flexors of the trunk have become more powerful; the abdominal muscles extending over the knees have restricted the movements of the femur. As a further result of this restricted movement the pelvis has begun to degenerate, the symphysis pubis become less defined, and the femur shortened. We are therefore, I submit, the actual witnesses of a process in the pinnipeds which if carried still further would bring about the condition now found in living cetaceans. The pedes in pinnipeds have been hypertrophied together with the metapodial and phalangeal elements, but are not the fingers also lengthened and their joints multiplied in the cetacean manus? In the Plesiosauri, Ichthyosauri and Lyrifera or true fishes, the same thing has occurred, namely hypertrophy and lengthening or increase of limb-elements comparable to phalanges, with a corresponding shortening of the proximal bones in contact with

the shoulder and hip-girdles. Manifestly the pes of a form like *Megaptera*, if mobile, would require a system of phalanges as powerful as those in the manus, but the pes is not mobile in any cetacean, on its own base, as is the fore-limb, but is rigidly affixed to the sides of the end of the tail and incapable of independent movement, hence the atrophy of its bones. The only evidence remaining to indicate that the pedes or flukes of cetaceans were once possessed of well developed phalanges, is the distribution of the dorsal and ventral interdigital arteries, the arrangement of these in fact indicating that there was a great inequality in the length of the digits of the pes, the same as we now see in the manus, thus leading to the conclusion that the foot-structure of the ancestral or protocetacean type was so far different from that of the pinnipeds.

The next step in the process would be the atrophy of the limb-bones and muscles, which, on account of still greater restriction of their movements, would become useless, leaving the integuments of the feet as the flukes on either side of the end of the tail, which, with the total abandonment of the land by the animal, would become stronger and its centra greatly developed, carrying the pedal folds or flukes still farther rearward, and thus increase still more the interval between them and the remnants of the pelvis. At the same time, the muscles of the tail would become greatly developed, so that in the cetaceans we actually have the spectacle of an animal type which has descended from a land form with a degenerate tail again acquiring a tail of the functional importance of that of a fish, but structurally very dissimilar, especially as regards the arrangement of its muscles, which are not homologous with the muscular somites of a fish's tail. The pes thus becomes the only outwardly apparent part of the hind limb, just as the manus is the principal part exserted in the fore-limbs of cetaceans, where some of the muscular insertions have also been shoved outward or into a more distal and effective position. The inclusion of the end of the tail of cetaceans between the flukes has also differentiated the caudal vertebrae of the latter into two distinct and well-marked series, so that the centra, as respects their vertical diameters, do not taper from the sacral region backward, as in other mammals, but only from in front of the flukes backward.

The arrangement of the vessels of the manus and flukes is somewhat similar, but totally unlike that of the vessels entering the dorsal fin, which has only a median system, whereas the flukes have about ten dorsal and as many plantar vessels just under the integument, the prolonged fourth of these, reckoning from the anterior border of the fluke, being the analogue of the prolonged interdigital artery lying between the second and third digits of the manus, and which supplies the end of the flipper with blood, just as the outer two-thirds of the flukes are supplied by the prolonged fourth dorsal and ventral pair spoken of above.

Finally, it may be said that the rudimentary tibia, when present, is directed backward in the cetaceans just as in pinnipeds, showing that if it were fully developed and prolonged it would carry the pedes far behind a vertical line drawn through the hip-joint. There is also other evidence that the inclusion of the hind limbs in the whales has occurred in much the same way as in pinnipeds, for example, the femora are adducted to a remarkable degree in *Balaena*, according to Struthers, showing that the encroachment of other parts must have been the principal cause of such adduction. The femora of *Halitherium* seem also to have been directed backward toward the flukes, according to the figures given by Lepsius.

The translocation of the pedes of cetaceans has been accomplished through an extended phyletic series and was not sudden or partially saltatory as in the case of the pelvic limbs of embryo physoclists. The translocation in the first case was due to the backward extension of the limb, outwardly carrying only the pes away from its original place, in the latter the whole limb is shifted together with the girdle. In cetaceans there has been little or no shifting of the pelvic girdle, its detachment from the vertebral column being due to the atrophy of the ilium. The extension backwards of the limbs and pedes parallel with the caudal portion of the vertebral column, obviously began in an amphibious mammalian type and has thus *gradually* brought the pedes to their present position, where they appear ontogenetically; heredity, through immediate ancestry, here, as in many other cases, greatly marring the phylogenetic record. This gradual shifting, according to the method described, completely does away with the difficulty suggested by Flower as to the helplessness of the animals during the transfer, which really began in forms already to a great extent helpless on land but certainly not in the water.

The foregoing gives the principal anatomical and embryological grounds for regarding the flukes of Cetacea as the representatives of pedes translocated backward by rotation and extension of the limb rearward into a position parallel with the tail by the process of inclusion as described above, but as it is impossible to consider the evidence in favor of this conclusion in detail in this brief abstract, those interested are referred to my illustrated memoir on the subject almost ready for publication by the U. S. Fish Commission.—*John A. Ryder.*

(From the *American Naturalist*, June, 1885.)

EMBRYOLOGY.¹

ON THE FORMATION OF THE EMBRYONIC AXIS OF THE TELEOSTEAN EMBRYO BY THE CONCRESCENCE OF THE RIM OF THE BLASTODERM.—During the season of 1881, I had an opportunity to study part of the developmental history of *Elacate canadus* at Cherry-stone, Virginia. But unfortunately the lot of ova investigated by me did not develop to the period of hatching, but only passed a little beyond the stage when the blastoderm closes. As I have referred elsewhere to the very remarkable condition of affairs observed by me just previous to the closure of the blastoderm in this species, and not being likely to soon again have an opportunity to study the same form, I will now describe and figure what

¹ Edited by JOHN A. RYDER, Smithsonian Institution, Washington, D. C.

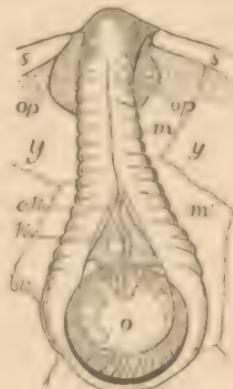
was then observed in a number of ova, from which I infer that the peculiarity about to be described is characteristic of the development of this form. This species hatches in 24 to 36 hours.

The accompanying figure represents the embryo lying on the surface of the vitellus, and is represented as foreshortened, anteriorly the optic lobes, *op op*, on the other side of the vitellus show through the transparent yolk. The embryonic axis shows the segments or somites, *m*, distinctly developed, but it is very remarkable that the segmentation does not end at the point where the axis of the embryo so far formed ends. The right and left limbs of the blastodermic rim form a Λ -shaped mass, together with the embryonic axis anteriorly, but unlike any other normal teleostean embryo both these limbs of the rim are distinctly segmented for some distance as at *m'*.

Just within the yolk and a little in front of the yolk blastopore, which runs forward into the acute angle formed by the limbs of the blastodermic rim, *br*, lies the large oil drop, *o*. A lozenge-shaped mass of cells lies in the acute angle of the Λ -shaped terminal part of the embryo, which appears to contain or overlie Kupffer's vesicle, *Kv*, and what was assumed to be the chorda, *ch*, at the time the observation was made, but of the certainty of this determination I am not at present satisfied. I was enabled to sketch this and a slightly more advanced stage several times, and as already stated found the same condition in a number of embryos, which seemed to be developing normally. Four other sketches show that the blastoderm finally closes very much as in other teleostean embryos and that pronounced wrinkles radiate from the crater-like opening upon the yolk where the yolk-blastopore finally disappears.

The conclusions of His and Rauber to the effect that the embryonic axis is formed by the gradual fusion from before backwards of the inner edges or the lips of the yolk-blastopore, as it advances over the surface of the vitelline globe, are in this case evidently correct, though it must be admitted that the presence of the cellular mass between the limbs of the blastodermic rim where they join the embryonic axis is not a little puzzling.—*John A. Ryder.*

THE MODE OF FORMATION AND THE MORPHOLOGICAL VALUE OF THE EGG OF NEPA AND NOTONECTA.—In the last number of the *Ztschr. für wissenschaftl. Zoologie*, 1885, xli. (p. 311), Ludwig Will has an article on this subject and reaches the rather startling conclusion that an egg-cell is not necessarily a simple protoplast, but may, while on the way towards the development of the ripe

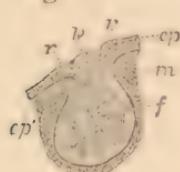


egg, give rise to other cells. In fact, the central chromatin body of the primitive egg-cell, which he calls the *oöblast*, ejects a large number of chromatin pellets from its substance which become the nuclei of the cells forming the egg-follicle. The conclusion at which Will arrives after reviewing the work of Fol, Roule, Sabatier, II. Ludwig, Balbiani and others, that in the ascidians, myriapods and insects, the nuclei of the follicular epithelium owe their origin to the primitive germinal nucleus or the *oöblast*, also holds good in respect to the ova of birds and amphibians, is of great interest, and stands in sharp contrast to the old view that, the ovi-cell and epithelial cells of the follicle were both originally similar elements (germ-cells), but which have merely developed farther in widely different ways.

Will summarizes his results as follows: 1. The nuclei of the follicular epithelium are formed from the *oöblast*. 2. The residuum of the *oöblast* becomes the germinative vesicle of the egg. 3. Ova which are without a follicular epithelial investment, as is the case in numerous groups of animals, are homologous only with the egg plus the follicular epithelium of the higher forms. 4. The egg of the Hemiptera is neither a cell nor an assemblage of cells, but the *product* of several cells. 5. The homological value of the eggs of different types is to be found in the fact that, in every case the ripe egg represents a germinal mass, in which are contained all the capabilities of future development, and which is the *product* of the activities of those cells which have shared in its construction.

ON THE DEVELOPMENT OF THE MAMMARY GLANDS OF CETACEA.—The following is an abstract of an account of some researches just completed for publication upon this subject, founded upon materials in the U. S. National Museum.

In cutting longitudinal sections of the tail of a female embryo of *Globiocephalus melas*, two inches long, the microtome cut through the incipient mammary glands, one of which lies on



either side of the external genital opening. The direction of the plane of section is nearly vertical and transverse judging from the appearance of the consecutive series. The accompanying cut will give the reader some idea of the appearance of these organs at the time

they begin to be involuted or formed as thickenings of the epidermis of the young fetus of these huge mammalia.

The outer corneous layer of the epidermis or epiblast, *ep*, and the lower layer of the latter on the Malpighian stratum, *ep'*, are alone concerned in the formation of the first rudiments of the mammae, as in other mammalia. Although but a single stage was investigated, and not being aware of the existence of any previously published researches upon this subject, it has been thought best

to give my results together with such other information as could be gathered from the examination externally of the mammae of a female whale's fetus, five and a-half inches long, belonging to the Pacific genus *Rhachianectes*. The stage here figured displays the gland in the undifferentiated condition of the five-months' human embryo, when the gland consists merely of an involution of the malpighian layer, *ep'*, filled by a solid core of more rounded cells, *f*, which seem to become blended, at the lower end of the involution, with the Malpighian layer, the whole structure presenting the appearance of a solid pyriform body jutting down into the mesoblast, *m*, and connected with the epidermis externally by a narrow pedicel.

No signs of the outgrowth of the rudiments of acini from this pyriform body have yet appeared, but it would be inferred from the shape of the gland in the adults that these acini would be most apt to first appear at the anterior and posterior sides of this body. The gland in the adult cetaceans is greatly elongated, flat and less than one-third as wide as long, reaching the enormous dimensions of ten feet in length, three feet in width and eight inches in thickness in the adult, gravid female of *Balaenoptera sibbaldii*. In the adult the gland is also traversed longitudinally by a spacious lacteal sinus, which is probably developed during the growth of the gland by a process of vacuolization. This sinus opens externally through the nipple by way of a single duct. The gland therefore probably belongs to that subdivision of mammary organs provided with pseudo-nipples, which are developed by the production of the edge of the embryonic mammary area into a tubular teat traversed by a single canal as in the cow, certain marsupials and rodents.

In combination with the peculiar internal structure of the mammary gland of cetaceans, there is also an external teleological modification of a remarkable character, the nipple itself being lodged in a cleft or fossa, and concealed from view from without by a pair of longitudinal folds which close over it. From the evidence presented by my sections of the stage here figured of the development of the mammae of *Globiocephalus* when compared with the condition of these organs in the relatively older female embryo of *Rhachianectes*, already mentioned, it would seem probable that these folds were developed very early, as the nipple rudiment or mammary area, *p*, has a fold on either side of it, represented in the figure by the elevations, *rr*, because in the larger embryo of *Rhachianectes* the mammary fossæ are already developed, and there are no externally visible indications of nipples under or between the folds, the cleft being still very short in this specimen, or only about 0.5 millimeter, being absolutely minute as compared with the mammary fossæ of the adult, in which they must be over a foot in length.

It thus becomes evident that the mammary glands of cetaceans

develop at the start in much the same way as those of other Mammalia, but that their evolution is complicated somewhat by the early appearance of the folds on either side of the mammary area, which grow upward to form the sides and roof of the fossæ, which eventually enclose the nipples. The condition of the still earlier stages of the gland, judging from the general appearance of my sections, must be very similar to that observed in other mammals by Huss, Langer, Kölliker and others.—*John A. Ryder.*

(*American Naturalist Extra, August, 1885.*)

EMBRYOLOGY.¹

ON THE AVAILABILITY OF EMBRYOLOGICAL CHARACTERS IN THE CLASSIFICATION OF THE CHORDATA.—The development of a median axial cord, differing essentially from cartilage, and which seems to arise from a strand of cells constricted off longitudinally from the upper side of the hypoblast and having the same or almost the same extension anteriorly and posteriorly as the nervous cord, at once distinguishes all embryo and primitive Chordata from all other types, and justifies the substitution of the latter term for the older name, Vertebrata. It is obvious that the term Chordata is a more applicable one for the reason that there are forms which never develop vertebrae, while there are none in this series which fail to develop a notochord at some stage, having the antero-posterior extension described above. The name Vertebrata, therefore, carries with it implications which are not justified by facts. Lankester insists for this reason that the term Vertebrata be abandoned, and that the word Chordata be substituted for the name of the phylum, so as to express a fundamental truth in scientific taxonomy.

It has been insisted that embryological data are not available for the purpose of discriminating classes, subclasses, etc., and, judging from the more or less unsatisfactory attempts made to arrange the Chordata on a purely embryological basis, this opinion has not been without foundation. The following notes are not so much intended to bring a new system to the notice of naturalists as to arrange some of the data of embryology in what seems to the writer a rational order. While it must be admitted that our knowledge is still imperfect in relation to the develop-

¹ Edited by JOHN A. RYDER, Smithsonian Institution, Washington, D. C.

ment of certain considerable groups, every addition to that knowledge demonstrates that what has appeared to be exceptional or in violation of general principles, upon further investigation has really substantiated those principles. Inasmuch as the theory of evolution, as well as that of embryology, first considers the simplest phases of differentiation, the order in which the types should be successively considered will be an ascending one, in which we will pass from the least to the most differentiated modifications of the egg and embryo, without admitting, however, that the order of arrangement here adopted is indicative of the exact course which the evolution of the groups has taken. That is a problem which for obvious reasons no one will probably ever solve or succeed in stating with more than partial accuracy. The scheme which follows is therefore offered merely to show the arrangement which results when embryological characters alone are used, and will, the writer believes, serve at least to bring together the principal facts so as to display the direction along which specialization has progressed in the course of the evolution of the modes of development of the various chordated forms.

The Chordata present three well-marked modes of embryonic development consequent mainly upon the manner in which the germinal matter of the egg is related to the vitellus, and upon how much the latter takes part directly in the formation of the embryonic organs, and in what manner the blastula or blastosphere is directly related to its environment in the course of its development and growth. The direct influence of conditions which induce modifications in a purely mechanical manner is very plainly illustrated in embryological development; in fact it may be shown that the highest type of development as displayed in the greatest complexity of the germ or embryo has grown out of a simpler condition developing under simpler environing conditions. It may thus be shown that *even the mode of development of the ovum has been modified through adaptation.*

I. The lowest and most unmodified expression of chordate development is that which I will call the Haplocyemate, as seen in the single type Branchiostoma. Here the embryonic axis develops directly from a double-walled gastrula formed by the invagination of one side of the blastula into the other half. The myotomes are developed from paired diverticula of the mesenteron, and the development is not modified in any way by the presence of a yolk-sack. This group embraces forms in which no part of the ectoblast is cast off when the embryo is set free, and in which there are no special respiratory saccular membranes developed in connection with any part of the blastula or blastodermic vesicle; no primitive streak.

Ovum with a zona radiata only, which becomes distended and tensely filled with water around the egg proper; no albuminous

envelope and no outer shell or additional membranous covering. Cleavage total and equal, as a result of which a blastula is directly developed. The invaginated half of the blastula leads directly to the formation of the intestine. No actinotrichia or embryonic fin-rays developed. These features seem to distinguish the Leptocardii, or Haplocremata forms from the succeeding ones.

II. The second great subdivision of the Chordata I will call the Epicyemata subphylum. In this series the embryo never becomes bodily invaginated or so pushed into the blastodermic vesicle as to become invested by up-growing folds of the ectoblast, but remains attached to the yolk by a stalk or is sessile upon and external to the latter, which may or may not form an integral part of the intestine. This group also embraces forms in which no part of the ectoblast is cast off when the embryo is set free. There is no amnion nor any functional allantois developed. The vessels of the yolk-sack, when developed, are respiratory in function. The primitive streak is either comparatively short or wanting. This subdivision answers very nearly to the Ichthyopsida of authors.

1. The lowest division of the Epicyemata series may be called the Ichthyoidea, and brings the Amphibia and Marsipobranchii together. In them the ovum is provided with a zona radiata; there is no outer albuminous envelope; the zona is often elastic, and the cavity it encloses may increase with the progress of development, and may be covered externally with an adhesive or gelatinous investment. The cleavage is unequal; no true blastodisk is formed; the germinal and nutritive poles are, however, soon defined at opposite poles of the egg. Vitellus segmented into large spheres which enter into the formation of the inferior portion of the intestinal wall. Oviparous, or the ova are carried about by the parent in dermal pouches.

a. The first subseries of the Ichthyoidea is enterotrophous, that is, the yolk cells in the embryo are in a ventral position, and extend along the whole of the middle and posterior part of the developing intestine. *Amphibia.*

b. The second subseries of the Ichthyoidea are opisthotrophous, that is to say, the yolk-cells while they enter into the formation of the ventral portion of the intestinal wall as in *a*, they are in a posterior position; the embryonic axis is formed from behind forwards, so as to appear as if it grew out from the posteriorly-placed mass of yolk-cells. *Petromyzon.*

Much may be said in favor of affiliating the marsipobranchs with the amphibians, but whether the development of *Myxine* will countenance the foregoing arrangement remains to be learned. It is, however, very certain that the general plan of development of the two preceding series approximates that of *Branchiostoma* far more closely than the more specialized development of the Ichthyes.

2. The highest major group in the Epicyemate subphylum I will call Ichthyes, as it is the only series in which true fin-rays are developed, and in all of the forms embraced by the term true embryonic fin-rays, or actinotrichia, may be found in the fin-folds of the embryo.

The ovum is provided with a *zona radiata*, but is entirely without or has only an inconsiderable albuminous envelope, rarely with loose granules of proteinaceous matter included between the *vitellus* and *zona*; no *chalazæ*; no calcareous shell, though sometimes there may be present in addition an outer tough, fibrous envelope (Elasmobranchs), or a canalculated gelatinous (*Perca*), or a partially separate adhesive investment (*Amiurus*). The cleavage is partial, but a well-defined blastodisk is developed: the blastosphere is formed by epiboly or growth over the *vitellus*. The vitelline matter is contained in the inferior pole of the blastosphere, but never enters directly into the formation of a part of the intestinal wall.

a. The first subordinate group under Ichthyes is characterized by being ectotrophous, for the reason that the embryo is sessile for only a short time, as it soon becomes folded off from the yolk and raised upon a hollow umbilical stalk, so that the yolk eventually occupies an apparently extra-abdominal position, or rather it lies in a bulbous extension of the abdominal cavity. This series embraces the Selachians and Holocephali.

b. The second subdivision of the Ichthyes is equivalent to the Teleostomi of authors. These, as far as known, are *cœlotrophous*, that is to say, the embryo is sessile upon the yolk, and is never folded off so as to develop a stalk; the yolk is intra-abdominal and below the intestine and between the latter and the greatly distended somatopleure.

The Teleostei, Holostei and Chondrostei belong here, and it will be very surprising if any embryological characters are ever found which will separate the archaic Crossopterygians and Dipnoans from this series. For the characters of the latter we must, however, await the results of the researches of Mr. Caldwell.

III. The third subphylum of the Chordata is Endocyemate, that is, the embryo is more or less completely invaginated into the blastodermic vesicle at an early stage, in consequence apparently of its being confined in a contracted space, such as the uterine cavity or outer egg-membranes and shell, as a result of which are formed from the ectoblast, during the further growth of the embryo: (1) the amnion and its cavity, (2) the false amnion and its cavity; into the resulting space between these two membranes the allantois and umbilical vesicle are extended. The primitive streak is usually more or less prolonged behind the embryonic axis. This subphylum embraces forms in which a part only of the ectoblast enters permanently into the formation of the embryo, while a larger portion from which the false

amnion or the *Reichert'sche Deckschicht*, Rauber, subzonal membrane, Turner, serous envelope, von Baer, and the true amnion, are formed, is cast off at birth or when incubation is completed. A highly vascular allantois is also developed in the majority of the species of this group, and, as a rule, takes the most important share in the respiratory functions of the embryo, and in the development of the fetal part of the placenta whenever that organ is present.—*J. A. Ryder.* [To be continued.]

(*American Naturalist Extra, September, 1885.*)

EMBRYOLOGY.¹

ON THE AVAILABILITY OF EMBRYOLOGICAL CHARACTERS IN THE CLASSIFICATION OF THE CHORDATA [*concluded*].—1. The lowest major subdivision of the Endocyclemate subphylum embraces forms in which the ovum is invested by a *zona radiata*, external to which comes an additional investment of albuminous matter secreted by the oviduct, this albuminous envelope being usually in turn covered by a fibrous membrane immediately overlaid by a porous, more or less calcareous shell, also secreted by the oviduct. Chalaza are often developed. The cleavage is partial, the germinal matter, as a rule, forms but an insignificant part of the whole ovum, and is aggregated at one pole of the latter as a blastodisk. The blastodermic vesicle is developed from the blastodisk by epiboly upon the vitelline mass, which is finally included so as to occupy a ventral position in the vesicle. Development is at most viviparous only during the very earliest stages or while the ovum is passing through the oviducts, or more or less entirely oviparous, or quite ovoviparous. The allantois is greatly developed, but never associated in the development of a true placenta, though it is usually respiratory in function.

Under this definition the three following groups seem to be appropriately included:

a. Ova buried in the earth or sand by the parent, and left to be incubated by the heat of the sun. Some species ovoviviparous. *Reptilia.*

b. Ova incubated by the parent in a nest specially constructed for the purpose. *Aves.*

c. Ova incubated by parent in an abdominal marsupium or in a nest at the end of a burrow. Recently hatched young nourished by the parent for a time upon milk secreted by mammary glands. No functional uterus. *Ornithodelphia.*

It may also be noted that with group *b* the distinctly warm-blooded series of the Chordata begins. The relatively high temperature of the body of the adult plays an important part in incubation or in accelerating metabolism in the embryo. The preceding three groups, on account of the many features of resemblance and reptilian traits possessed in common (group *c* being apparently affiliated with the extinct Theromorpha of Cope), might be considered to form a series to be called Paratheria.

d. The highest major subdivision of the Endocyclemate sub-

phylum embraces the eutherian type, or the viviparous Mammalia, in which the ovum is invested only by a zona radiata. The ovum also becomes more or less covered over by reflections of the uterine epithelium, or processes from the surface of the ovum are received into furrows or pits of the mucous surface of the uterine cavity, in which embryonic development proceeds more or less nearly to completion, and where the developing embryo acquires nourishment after the manner of a parasitic organism. The cleavage of the egg is total, and leads to the formation of a hollow, rapidly-enlarging, blastodermic vesicle or blastula, in which no vitelline matter or deutoplasm lies free in the ventral pole or yolk sack. This group is characterized by its viviparity, the development of a placenta and the possession of a functional uterus; it has obviously descended from one of the preceding groups which had ova provided with a large yolk, the yolk having gradually atrophied or failed to develop as the peculiar viviparous mode of development became more and more pronounced.

a. The lowest division of the Eutheria would be separated from the highest, on embryological grounds, by the circumstance that the vascular system of the foetus is brought into relation with the maternal vessels by means of the vessels of the yolk sack (Owen, Osborn). Or by means of pseudopodal processes of the cells forming the yolk sack, *Phascolarctos* (Caldwell). Allantois more or less rudimentary. *Didelphia*.

b. In the highest division of the Eutheria the vascular system of the foetus is brought into relation with the maternal vessels by means of the allantois, which is concerned in forming a villous or spongy vascular mass known as the placenta. *Monodelphia*.

In the present state of our knowledge it seems premature to attempt a definition of the orders of the Monodelphia upon the basis of placental characters alone, as the following scheme seems to show. It is difficult, however, not to believe that the non-deciduate and diffuse type of placenta is the most primitive, and that then follows the deciduate zonary, and finally as the most specialized the deciduate discoidal. This seems to me must have been the order of evolution of the forms of the placenta, for the reason that in the Paratherian, Endocystemate form, from which the Eutheria have undoubtedly been developed, the vascular allantois invests the whole embryo. In this succession the orders of the Monodelphia will therefore be here arranged as nearly as possible:

aa. Placenta non-deciduate, diffuse or cotyledonary. *Cetacea, Sirenia, Ungulata.*

bb. Placenta non deciduate, diffuse (*Manis*) ; or non-deciduate ? nearly zonary (*Orycteropus*) ; or non-deciduate, zonary (*Dasyurus novemcinctus*) ; or deciduate discoidal (*Dasyurus* sp., *Choloepus*). *Edentata*.

cc. Placenta deciduate, zonary. *Carnivora, Proboscidea, Hyracoidea.*

dd. Placenta deciduate, discoidal or exceptionally non-deciduate and diffuse as in the Lemuridae. Rodentia, Insectivora, Cheiroptera, Primates.

Much remains to be learned of the earliest stages of the formation of the placenta, especially in the Primates. In *Talpa*, Heape has found a rudimentary "träger" or suspensor developed. In some of the Rodentia the embryonic mass is precociously invaginated into the blastocœl, and the amniotic cavity is formed in the most extraordinary manner, or by a sort of vacuolization or accumulation of fluid (*liquor amnii*) in the midst of the mass of undifferentiated embryonic cells. This occurs in *Mus*, *Arvicola* and *Cavia*, according to Selenka. In these forms the blastodermic vesicle also becomes adherent to the uterine epithelium at a very early stage, and the suspensor is very markedly developed in the three forms mentioned. The precocious invagination of the undifferentiated embryonic mass of cells into the blastocœl leads, in the Rodentia, to an apparent inversion of the embryonic layers. These forms have therefore attained the most specialized mode of development known amongst Mammalia, so that, judged by the standard of embryology alone, they would rank higher than the Primates.

The foregoing scheme illustrates in a very striking manner the way in which complication after complication has been added to the developing germ, starting with a simple blastula developed by total cleavage in *Branchiostoma*; the next step in the progress of embryonic specialization is that seen in the amphibian and marsipobranchian embryo, in which a distinct neurenteric canal is also developed, and in which the neurenteron is continued into the enteric cavity, which itself traverses the segmented vitelline mass longitudinally along its upper half. In the next grade of specialization, or that represented by the Ichthyes of this arrangement, the vitellus remains unsegmented for a long time, and is practically excluded from sharing in the formation of the enteric walls, but the embryo is sessile in the greater number of species embraced in this series, and while only a portion of the blastodermic area leads to the differentiation of an embryo, no part of the ectoblast is ever so folded off to form provisional organs such as the amnion and false amnion, which serve only a temporary purpose, to be finally cast off when they have subserved their function in the development of the embryo, as in the highest forms. These latter, or the endocyemate types, as a rule, develop a blastoderm with a relatively very large area, but only a very small portion of the ectoblast ever takes a permanent share in the formation of the body of the embryo, the remainder of this layer being entirely deciduous. In the Paratherian series of endocyemate types, viz., Reptilia, Aves and Ornithodelphia, there is a large yolk developed, which seems to have determined the development of the hollow yolkless blastosphere of the Eutheria, in which, how-

ever, there is a manifest tendency for that structure to increase rapidly in size owing to the imbibition of fluid with which the blastocœl becomes more and more distended, this increase in size at the same time being aided by the division of the cells entering into the formation of the walls of the blastocœl. The greater part of the walls of this vesicle are finally metamorphosed by a process of folding off and ingrowth of the embryo into the vesicle by invagination, into a respiratory apparatus and secondary system of envelopes, a portion of which also takes part more or less extensively in the absorption of pabulum from the surrounding uterine surfaces which may be more or less completely reflected around the embryo and its vesicle, to be finally cast off at birth together with those parts of the vesicle derived from the ectoblast, which are also deciduous. The vesicle also tends, with a few exceptions, to thrust out hollow villi, which dip into pits in the uterine mucosa. These may arise locally or all over the vesicle, and reach their fullest development when the chorion has been formed, when the greater part of the surface of the vesicle acquires a shaggy covering of villi, into which vascular loops from the allantois are insinuated, over a restricted area internally or over its whole surface. These then become more or less completely insinuated into vascular uterine crypts into the constitution of which a decidua may or may not enter.

It will, I think, be obvious to any one, that if an oviparous paratherian form were to have the eggs which it produces so modified as to lose the shell, yolk and albuminous and fibrous envelopes, leaving only the naked endocymate ovum to be retained near the outlet of the oviduct, the wall of which would then become thickened so as to form a specialized uterine dilatation, the conditions for a realization of the eutherian mode of viviparous development would be present. In this way, no doubt, the peculiarly specialized mode of mammalian development arose.

Objections may be urged against the position I have assigned to the Amphibia and Marsipobranchii as well as to the names given to the groups, and to the stress laid upon the physiological aspects of development and their importance not only in taxonomy but also in tracing the mode of the evolution of particular grades of development.

The form of the placenta seems to depend upon several factors: (1) The early or late attachment of the blastodermic vesicle to the uterine walls; (2) the early or late invagination of the embryo or embryonic mass; (3) the extent of subzonal membrane covered by the allantois, and the mode in which the latter is extended; (4) the form of the uterine cavity in which the blastodermic vesicle is lodged, whether tubular, bicorned or irregular; (5) the position and disposition of the uterine mucosa which is brought into relation with the placenta, whether it lines the conical or tubular

cornua, sides or fundus of the uterus; (6) the disposition of the crypts, fossæ, pits or folds of the uterine mucosa; (7) the arrangement and disposition of uterine vessels from which the maternal tufts or villi are fed and derived. These influences are largely mechanical in character, and like the influence exerted by the *vitellus*, lead, in certain cases, to very remarkable modifications of embryonic development.

The foregoing scheme deals more especially with the evolution of the various higher types of development, and if the way in which these have grown out of the lower ones has been made a little less obscure than hitherto, my object in writing this will have been attained. The manner in which placentation has been modified is also a fruitful subject for farther investigation, not less so, in fact, than the question as to how the amnion arose. The facts of embryology tend to show that the amnion is the result, as stated above, of the gradual invagination of the embryo into the blastodermic vesicle. The invagination begins at the head end of the embryo; the amnion, as is well known, always developing its first traces at the cephalic end of the embryonic disk. It is also probable that the cavity of the false amnion is the homologue of the cleavage cavity of certain of the lower forms.—*John A. Ryder.*

(*American Naturalist Extra, November, 1885.*)

EMBRYOLOGY.¹

THE ARCHISTOME-THEORY.—The new doctrine of development, of which it is proposed to give a brief and partial sketch here, rests in part on a hypothetical basis and in part upon a well established theory founded upon observation. It consists further in an expansion and adaptation of the gastræal-theory of Haeckel in the light of more recent research, and a reconciliation of it with the deductions of His, Rauber, Whitman and myself, as to the occurrence of concrecence of the lips of the blastophore and the differentiation of the axis of the body of the embryo from behind forwards, generally of bilateral types with paired mesoblastic sacks derived

¹ Edited by JOHN A. RYERSON, Smithsonian Institution, Washington, D. C.

directly or indirectly from the archenteron. It is also assumed with Sedgwick¹ that the most primitive form in which an imperfect approach towards the differentiation of a body-cavity is evident, as paired pouches of the archenteron, still opening into the latter, is seen in the bilaterally differentiated Actinozoa. It is further assumed that this modification of the archigastrula, as the primitive gastrula may be called as defined by Haeckel, is the first intimation which we have in any existing type, permanently represented in the ascending scale of morphological differentiation of organisms, of the permanent assumption of bilaterality. It is also assumed with Sedgwick that the mouth of such a form was elongated in an antero-posterior direction, thus leading to the differentiation of a permanent mouth and anus at the opposite ends of the original slit-like mouth of such a form. The circumoral band of sensitive tissue is also assumed to have given rise to the median nervous system of Chordata and Achordata. In the former median concrescence of the originally paired cords has been complete, and in the latter incomplete, so as to give rise to circumoral and circumanal nerve rings and a pair of ventral ganglionated cords. It is thus made obvious that I assume in a general way that the hypotheses propounded by Sedgwick are supported by a very large body of evidence and enable us to interpret and reconcile with great readiness the conclusions of biologists in reference to the development of other structures, especially the excretory, generative and appendicular organs. The evolution of the first two, the trachea of insects, the branchiæ of various forms, abdominal pores, muscular somites, etc., has been more or less fully discussed by Sedgwick himself, but the probable source and genesis of the limbs and appendicular organs he has hardly more than alluded to. To this part of the subject and the nature of the gastrula of bilateral forms I shall therefore especially address myself, and I hope greatly expand and further emphasize the views of Balfour's very worthy successor.

The antero-posteriorly elongated primitive gastrula mouth or blastophore of bilateral forms is assumed to have become secondarily elongated, either by a direct and obvious process of median concrescence of its lips, as in Clepsine, in fishes, in Peripatus and arthropods generally, or this has become greatly obscured, as in Balanoglossus, Branchiostoma, Chætopoda, Chætognatha and some of the higher chordata and in certain degenerate types, as a result of secondary modifications which have immediately affected the primary sequence of events in the development of the neural plate or medullary groove. I therefore assume, in effect, that the medullary plate in all forms has been primarily formed from the concresced lips of an elongated blastopore, and this has in the

¹On the origin of Metameric Segmentation and other morphological questions. Studies from the Morph. Laboratory in the University of Cambridge, II, 1884, pt. 1, pp. 77-116, pls. x and xi. Also in Quart. Jour. Mic. Science, 1884.

lower forms been very generally perforated in the median line anteriorly to form the permanent mouth, and posteriorly to form the anus. The secondary modifications which have affected this mode of development of the permanent openings into the enteron depend, apparently, in large part upon a change in the aspects of the body, especially in the chordata in which the permanent mouth and anus are both new developments and do not coincide with the mouth and anus of primitive Bilateria.

The primitively elongated mouth of the larvae of Bilateria, with an extended body-axis, or any derived form of the latter, or wherever there is formed a well defined, unpaired median neural plate, or where a pair of parallel neural plates or cords are developed, I would call the whole area thus embraced an *archistome*. In the higher forms this archistome would be coextensive with the neural groove antero-posteriorly, as far forward as the pineal body, and as far backward as the true secondary blastopore, and even beyond it, when a primitive streak was formed by the concrecence of the limbs of the blastoderm behind the posterior end of the axis of the embryo. In other words the archistome would extend from the pineal body in chordate embryos along the whole length of the embryonic axis through its blastopore and on through the primitive streak to the point where the yolk-blastopore closed. If the archistome were, therefore, to remain open, it would present the appearance of a cleft dividing the embryo into two symmetrical halves through the median line, and would extend even through the aborted portion of the lips of the primitive blastopore when a very long primitive streak was developed. It is thus rendered evident that I do not regard the unmodified, round gastrula-mouth, as understood by Haeckel, as always representing all of the blastopore in higher forms. According to this view the original gastrula-mouth is in fact greatly elongated as a result of growth in length, in consequence of which bilaterality becomes established, and of which we have the first hint in the Actinozoa. This is further intensified by development from before backwards, since, without exception, the elongate Bilateria differentiate the cephalic end of the body in advance of the caudal. In confirmation of the foregoing views I would refer the reader to the existing special memoirs on the development of the primitive grooves and blastoderms in the fishes and arthropods (Tracheates especially).

Furthermore, the phylogeny of the mesoblastic somites is absolutely untraceable to any other source except to the gut pouches of a bilateral type approximating the Actinozoa, and whether the process has been abbreviated in arthropods or not, we are at least certain that in some primitive Chordata, the Teleostei, for example, the proof that the mesoblastic somites of the body grow from the concreased lips of the blastopore are so conclusive as to be incontestable. The way in which the mesenteron arises, and

the manner in which the primitive cumulus is formed at the germinal pole of blastodermic vesicle of Arthropoda indicates, it seems to me, taking into account the fact that the mesoblast is split off from the lower side of the neural plate, that the mesoblastic somites are here formed in essentially the same way as in the Chordata. The invagination or folding in of the germinal area, in insect embryos to form the amnion, at first posteriorly and at the sides, or according to the plan just the reverse of what holds in the formation of the amnion in the endocystemate types of Chordata, is to me conclusive proof that concrescence of the lips of the primitive elongated blastopore, or archistome, has taken place; for, in order to effect this sort of an invagination of the embryonic area the head end must for a time remain fixed, while the tail, continuing to grow in length, is thrust into the yolk, as in *Calopteryx*, carrying the amniotic limb of the blastoderm before it. It also seems that paired cavities soon appear in the mesoblastic somites underlying and derived from the epiblast, as above described in arthropods. I therefore see no very essential difference in the method of development in the two types. In both it is obvious that a portion of the archenteric walls of the elongated archistome has given rise to the mesoblastic somites, by a process which differs in no respect from, but agreeing even in its abbreviation with that which takes place in *Branchiostoma* directly from the sides of the archenteron.

We now come to the consideration of the most important part of the archistome-theory, namely, that portion of it which deals with the genesis of the limbs and their musculature. The readiness with which the view that the tentacles of an actinozoan ancestral form gave rise to the integument and musculature of the paired limbs of the Bilateria is reconcilable with all the facts of embryology, is very remarkable. As is well known, the tentacles of *Actinia* consist of an outer layer of epiblast into which a hypoblastic lining is thrust from the paired lateral gut-pouches. If the gut-pouches of the actinian were now shut off from the archenteron we would have mesoblastic somites developed and structures formed which are exactly recapitulated in the development of the Arthropoda. That is, the outer layer in the budding appendages of the embryos of the latter, which grow out from each segment, are constituted of the same two layers, the outer of which gives rise to the hard, chitinous joints, and the inner to the muscles which move them.

In the development of bilaterality through the actinozoa the circle of tentacles would be drawn out into an ellipse, or so as to enclose an oblong space surrounding the archistome. This would bring the primitive appendages, after a free existence had been assumed by the supposed ancestral actinozoan type, into about the position in which they grow out in arthropod embryos around the archistome or furrow in the neural plate. The

post-anal telson or bristles, and the preoral labrum and one or two pairs of antennae may be supposed to have been derived from a postanal, and a preoral series of tentacles respectively, supposing of course that the mouth is formed from the anterior part of the archistome, while the anus is formed from its posterior portion, while, as supposed by Sedgwick, the middle portion has coalesced.

The biramous legs of Crustacea and certain insects may be supposed to have arisen from a bilateral actinozoan type in which there were two rows of tentacles encircling the oblong archistome. When the inner and outer archipodia of one side, as we may name these primitive limbs, had fused at their bases, we would have a biramous appendage. As the outer layer became chitinized these appendages would become segmented. A very primitive type of limb, which may be supposed to have been derived from the tentacle of an actinozoan ancestry, is found in *Peripatus*. The parapodia of worms may also be supposed to have been derived from two such circles of archipodia which surrounded the archistome, but which, as the body became elongated, assumed a more and more lateral position. A new set of structures are, however, developed in the parapodia of errant marine worms, the analogues of which are found only in the fin-folds of the embryos of osseous fishes, or as the rays of the most primitive and undegenerate types of adult forms, namely, the Elasmobranchii, Holocephali and Dipnoi. These structures are the setæ which are of epidermal origin in the worms, or at most subepiblastic; as in embryo fishes and in *Sagitta*. In a former number of this journal I have called these structures in fishes actinotrichia; these are the same as the embryonic fin-rays mentioned by A. Agassiz.

The principal reason why I consider the actinotrichia found in fish embryos analogous if not homologous with the setæ found in the appendages of worms, is the fact that in both cases muscular processes of the mesoblastic somites first become attached to the inner ends of these fine horny or chitinous filaments, which in the worms protrude beyond the margins of the soft tissue of the parapodia, but which in embryo fishes and in *Sagitta* do not extend beyond the edges of the fin-folds. It is thus rendered obvious that bundles of muscular fibers derived from the muscular somites, developed from lateral gut-pouches, pass outward and are inserted upon the proximal ends of the setæ found in the parapodia of worms as well as the actinotrichia found in the fin-folds of fish embryos. In fishes these muscular processes are given off to the actinotrichia of the unpaired as well as to those of the paired fins. These muscular processes moreover pass outward into epiblastic folds in both cases metamerically or from each segment. In the worm to a bunch of setæ in a single parapodium, in the fish to a bunch or longitudinal series of actino-

trichia to the number of a dozen or so opposite each segment. In fish embryos the actinotrichia finally have their proximal ends drawn together out of their original parallel position under the epiblast of the fin-fold, and radiate more or less markedly from the point where the muscular process from the mesoblastic somite is inserted upon them, the same as the diverging setæ in the parapodia of worms. This divergency gives rise to the dichotomous character of the bony rays of Teleost fishes, since, as I have shown in a previous article, the actinotrichia are the rudiments of the permanent osseous, segmented rays of the malacopterygian type. For these reasons I am very strongly inclined to believe that the parapodia of worms and the fin-folds of fishes are very intimately and probably genetically allied to each other.

Another strong reason for such a belief is that in *Sagitta* in which the transverse septa in the body-cavity have been obliterated, as in Chordata, the setæ are found, as in fish embryos, lying parallel with each other and in horizontal, lateral, continuous fin-folds. This would seem to indicate that *Sagitta* had descended from a worm in which a lateral row of parapodia had gradually become fused together serially by their edges so as to form a more or less nearly continuous lateral fold. And I see no reason to doubt that a similar longitudinal or serial concrescence of primitively distinct metamerous finlets may have occurred in the Protochordata, and given rise to the median and lateral longitudinal fold from which all of the fins develop. The next strong reason for this conclusion is that an actual longitudinal concrescence of the metamerous elements of the paired and unpaired fins of fishes actually occurs. This is especially obvious to any one who has studied the mode of development of the fins of fishes in which extensive longitudinal concrescence has taken place, and of which any one who will examine an adult skate may easily satisfy himself. In this form the pelvic and pectoral pairs of fins have been formed of a primitively continuous series of metamerous elements, as shown by the development. The anterior part of the lateral series of metamerous elements of the fin-fold in this type are crowded together at their bases to form a pectoral, the posterior part of the series of elements are in the same manner crowded together to form the pelvic fin. In this way it comes about that the rays and metamerous elements lose their original parallel position with respect to each other and become divergent distally, while the basal parts of the skeletal series of elements concresce or fuse to form the compound pro-meso and metapterygial pieces.

The lateral fins of fishes I regard as having arisen from the serially fused notopodial appendages of a worm-like ancestor, the unpaired fins in like manner I regard as having arisen from parapodia; the dorsal median fold from the two lateral rows of neuropodia which have concresced on the median line, and the ventral fold from the two rows of notopodia which have in like

manner fused together on the median line serially and transversely. The actinotrichia of all the fins are accordingly represented ancestrally in the slender embedded part of the parapodial setæ of worms.

These conclusions seem to support those of Dohrn, but also receive additional support from a consideration of the segmental organ and the way these are developed in certain worms, according to Hatschek, and in Chordata, according to Semper and Balfour. In one other important point the primitive Chordata and chaetopods agree, namely, in the possession of a great number of segments or mesoblastic somites. I therefore regard the Chordata and Chaetopoda as representing two divergent series. The former, upon the concentration of the muscular substance of the somites on the neural aspect of the body-cavity, and the abortion of the latter in the caudal region, acquired a new mode of progression, the tail then became vertically flattened, so that the parapodia were thrown into two rows dorsally and ventrally, and finally fused as supposed above; the displacement towards the middle line of the rows of parapodia being greatly favored by the lateral movements of the tail of the ancestral form. The presence of the body-cavity and viscera anteriorly probably prevented the shifting and median concrecence of the notopodia, so that they remain near their original position as the rudiments of the paired fins.

These views may at first seem far-fetched and improbable, but when I am able to present them more fully with new data and illustrations in a special memoir¹ upon which I am now engaged, I hope to be able to show that they lead to conclusions of the greatest possible moment in scientific morphology.—*John A. Ryder.*

¹ Studies on the development of the Chordata and Achordata, together with an exposition of the Archistome-theory.

EMBRYOLOGY.¹

THE DEVELOPMENT AND STRUCTURE OF MICROHYDRA RYDERI
POTTS.—The discovery and prolonged observation in the living state of this remarkable fresh-water cœlenterate, which is obviously allied to *Hydra*, is due to the painstaking care of Mr. Edward Potts, who found it adherent to stones to which fresh-water Polyzoa were attached, which he brought from Tacony creek, near Philadelphia. Mr. Potts has named the animal for the writer,² to whom he has also turned over three series of sections, prepared by Mr. Harold Wingate, from three individuals. Fortunately two of these series of sections, one a slide containing forty-two transverse, and another nine longitudinal sections, enables me to make a very thorough comparison with the structure of *Hydra* as displayed in a series of sections of *H. viridis* and *H. fusca*, from both of which Microhydra differs not only in size but also in histological details as well as in its mode of development. This singular organism also differs widely from the marine *Protohydra leuckartii* Greef, in being very much smaller, and in being an inhabitant of fresh water; it also differs from *Protohydra* in its method of reproduction by gemmation from the side of the body instead of by transverse fission. In this last

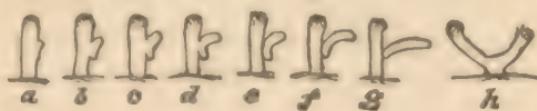
¹ Edited by JOHN A. RYDER, Smithsonian Institution, Washington, D. C.

² *Science*, Vol. v, 1885, No. 123, in the accompanying cover sheets, called the *Science Bulletin*, p. v, under the head of Recent Proceedings of Societies, the name *Microhydra ryderi* was first published, together with a brief account of its structure and habits, as a report of a verbal communication made by Mr. Potts at the meeting of the Academy of Natural Sciences of Philadelphia, held May 19, 1885.

feature, or in respect to its gemmiparous development, *Protohydra* agrees with the *Acraspeda* or *Discophora*, in multiplying by transverse fission, such as is seen in the asexual *Strobila* stage of the latter. In one important feature *Protohydra* and *Microhydra* agree, namely, in that neither form possesses the slightest traces of tentacles. The widely different habitats of the two forms, as well as their diametrically opposite methods of gemmiparous reproduction, leads me to the conclusion that they are not very closely related. Its affinities are clearly with *Hydra*, but that it cannot in any sense be regarded as a mere stage of the development of the latter, follows from other considerations which I will now state.

Its minuteness might very readily lead to its being overlooked. It measures alive .5^{mm} in height; the longitudinal sections in my possession are somewhat shorter, or about .475^{mm} in length, a difference probably due to contraction. Its diameter at the oral end is somewhat greater than at the base, and ranges from about .15 to .175^{mm}. In fractions of inches its dimensions are: height $\frac{1}{16}$ inch, diameter of body $\frac{1}{32}$ inch, constituting it the most diminutive adult hydroid or coelenterate type yet known, so that its generic name is especially appropriate. In life the animal is very much less contractile than *Hydra*, and is without the well-defined pedal disk of the latter or of *Protohydra*.

No sexually mature individuals of *Microhydra* have been found by Mr. Potts, who has, however, most laboriously and carefully studied the gemmiparous or asexual reproduction of the species in the living animal, he having been able, in fact, to watch this process in several successive generations. The asexual reproduction of *Microhydra* is, however, so very different from that of *Hydra* that there can again be no doubt of the absolute distinctness of the two forms in question. In *Hydra* the gemmiparously produced young animal, which is budded from the sides of the body, soon becomes pyriform, buds out tentacles and is constricted off from the parent by transverse fission around its base or pedal disk. In *Microhydra* a very different method of lateral gemmation occurs, since the bud very soon becomes sausage-shaped instead of pyriform, but it grows out from a swelling or thickening at the side of the parent the same as in *Hydra*. In *Microhydra* a constriction or furrow appears at either end of the young bud as soon as it is well defined as such. The gradual



Microhydra ryderi.

progress of the development of a bud is shown in Figs. *a*, *b*, *c*, *d*, *e*, *f* and *g*. The last shows the young *Microhydra* in the act

of being detached from the parent. These figures are from sketches by Mr. Potts as the process was watched by him at different stages. It is clear from these figures that the process of gemmation in *Microhydra* is very different from that seen in other hydroids; it is, in fact, as if both ends of the young polyp were being budded out of the side of the parent simultaneously, final separation of the bud occurring at one of its sides instead of at its base. The process thus actually makes something of an approach toward longitudinal instead of transverse fission.

The bud after detachment drops down upon an adjacent surface and for a time lies quite prone upon its side. It is entirely without cilia, in this respect resembling the larvæ of *Hydra*. It, however, seems possessed of slight powers of locomotion, which is effected probably by the contractions of the body. After lying in its prone position for a time, the vermiform body of the polype becomes fixed to the foreign object upon which it rests, by one end, while the other end is slowly raised into the erect position, when it may be said that the creature is adult. The history of the internal changes which the larva undergoes while budding are not known, but it is probable that the bud has the oral opening developed at its free end by the time it assumes the erect position.

Colonies of two have been observed by Mr. Potts, appearing somewhat as in the sketch in Fig. 4. This indicates that *Microhydra* in common with all other Cœlenterata has a tendency to form compound individuals or corms. Whether the stomachs of such compound individuals open into one another has not been ascertained, but it is extremely probable that they do. The preceding evidence, taken as a whole, it seems to me, leaves absolutely no doubt respecting the distinctness of the remarkable little organism discovered and so patiently studied by Mr. Potts.

The structure of the body in the *Hydra* and *Protohydra* agree pretty closely; in both there is an outer ectodermal layer, throughout which the nematocysts are pretty uniformly distributed. Under the ectoderm of both there is a thin layer consisting of contractile processes of the ectodermal cells. The endoderm consists in both of large vacuolated cells, containing excentrically placed nuclei and great numbers of granules at their inner ends. These large vacuolated, endodermic cells seem to line the whole internal cavity in both of the genera named.

In *Microhydra* the structure of the body is different from either of the preceding. There is a thin outer ectodermal layer, but the nematocysts are mainly aggregated at the oral end of the creature, few being present on the sides. Under the ectoderm there is a barely discernible thin stratum consisting very probably of the contractile processes of the outer layer cells. Around and just within the lips of the oral aperture the endodermic cells are solid. Just below the oral opening and for about one-third the

length of the animal, the endodermic cells are large and vacuolated as in *Hydra*, but the eccentrically placed nuclei are absolutely and relatively very much smaller than in *Hydra*. There is a gastric cavity extending down from the mouth for about the same distance, below which the alimentary cavity becomes less apparent and is surrounded by solid endodermic cells. These details are shown in both the longitudinal and transverse sections. In the cross-sections evidences of slight irregular foldings of the endoderm are present as in *Hydra*.

Greef has described a homogeneous cuticula covering the basal part of the ectoderm of *Protohydra*. A similar homogeneous cuticula seems to loosely invest the ectoderm in the sections of *Microhydra*. Mr. Potts, however, is not disposed to agree with me on this point, as he informs me by letter that he was unable to detect any such envelope in the living larvæ studied by him.

There is a distinct but small oral opening at the upper end of *Microhydra*, which is cleft-like or irregular, through which food is taken in, as observed by Mr. Potts. The gastric cavity is small and only the upper end of it appears to possess a specially developed digestive function. The digestive cavity of *Microhydra* is, in fact, but little more developed than in the later planula-stage of such a form as *Euope*. In fact, if the planula of the latter were to lose its cilia, become fixed and acquire a mouth, the morphological complexity of *Microhydra* would be realized. We have then in *Microhydra* an adult type which represents practically a planula which has acquired a mouth. In other words, the new type is not only the simplest of *Hydroids*, but is also the simplest of all true polypes or *Cœlenterata*. It is, in fact, a much more rudimentary form than even *Protohydra*, and represents perfectly a permanent gastrula which reproduces itself by lateral gemmation instead of by transverse fission.

It has been contended by some that *Hydra* is a degenerate form, and that *Protohydra* and *Microhydra* must be considered in the same light. As no very cogent reasons have ever been adduced in support of such a conclusion, I shall leave the *onus probandi* to be produced in favor of that view by those with whom it originated. The very simplicity of the type in question, it seems to me, must ever remain a serious bar to arriving at any very certain conclusions on this head. It seems as impossible to me to prove that *Microhydra* has been developed by the degeneration of a higher type, as it does to prove that it is a form which has advanced but very little beyond the planula stage of the *Cœlenterata*. The latter view seems to me to be by far the most probable, since it is a free-living form, which is no more likely to have been adversely affected than would hundreds of others living in the same environment. The significance of this singularly interesting type in relation to the question of the possible origin of the *Cœlenterata* is very great, and the interest which attaches to

it from the standpoint of the embryologist, it seems to me, fully warrants its discussion in this department.

With the help of Mr. Potts, who has generously given me permission to do so, I propose at an early date to prepare a more extended paper on this organism, with good illustrations. As it is, I must express my great obligations to its discoverer for the free use of many of the facts detailed above.—*John A. Ryder.*

[As this note on *Microhydra* goes to press, I have met with a paper¹, published in the *Proceedings Royal Society, London*, Vol. *xxxviii*, No. 235, Dec. 11th, 1884, pp. 9-14. According to this account, the supposed hydroid phase of *Limnocodium* is without tentacles; it was found attached to roots of *Pontederia* in the tanks of the Royal Botanic Society, Regent's park. The figures given by Bourne of the suspected hydroid phase of the singular fresh-water Medusa known as *Limnocodium*, are certainly very similar to *Microhydra*, but the former is larger than the latter and measures from $\frac{5}{16}$ th to $\frac{1}{4}$ th of an inch long. Colonies of three or four individual zooids were frequently met with. No true perisarc or cuticula was observed as in *Microhydra*, but the surface is covered with particles of mud and other débris, which becomes glued together by some secretion of the animal, and forms a sort of tubular casing. In internal structure this hydroid stage of *Limnocodium* differs considerably from *Microhydra*, however, judging from Bourne's description and figures. Is it possible after all that *Microhydra* is only the hydriform stage of fresh-water Medusa? If so, it is very probable that it may be allied to *Limnocodium*, the latter of South American origin, has in all probability a very different life-history from the North American *Microhydra*, if we may go so far as to assume that the latter has a medusiform adult stage. No lateral budding and dehiscence has been observed to occur in the supposed hydroid phase of *Limnocodium*, such as takes place in *Microhydra*, besides the larger zooids of the former were over six times as long as those of the latter, otherwise there are many striking similarities. Notwithstanding the existence of these resemblances, I think we may assume that if *Microhydra* should turn out to be only the hydroid stage of a mature medusa-form the latter will be found to be generically distinct from *Limnocodium*, in which case it might be called *Pottsia*.—*J. A. R.*]

¹ On the Occurrence of a hydroid phase of *Limnocodium sowerbii* Allman and Lankester, by Alfred Gibbs Bourne.

(*American Naturalist Extra, January, 1886.*)

EMBRYOLOGY.¹

THE DEVELOPMENT OF THE TOAD-FISH.—The development of the Batrachidae is not well known, as will appear from some of the statements in systematic treatises. One author states that: "The young of some or all the species fasten themselves to rocks by means of an adhesive disk, which soon disappears."

It is the purpose of this notice to point out that the adhesive disk referred to above is of a wholly different nature and origin from that found in the lump-fishes and Gobiesocidae in which such

¹Edited by JAMES A. KAYER, Smithsonian Institution, Washington, D. C.

a disk is formed by the confluence or coalescence of the pectoral pair of fins.

The adult toad-fish burrows a cavity under one side of a submerged boulder, and to the solid roof of this cavity the female attaches her ova in a single layer. The eggs are very adhesive and quite large, measuring about one-fifth of an inch in diameter. Like the male cat-fish, the male toad-fish assumes charge of the adherent brood of eggs and remains by them until they are hatched and subsequently become free.

The egg-membrane or *zona radiata* is very firm, and adheres to the under surface of the stone by a discoidal area about 3^{mm} in diameter. The free globular pole of the egg is accordingly directed downwards. The germinal disk is developed at the lower pole and gradually spreads so as to enclose the vitellus from below upwards. The result is that the embryo is formed upon the lower or free pole of the egg, where it develops until it finally ruptures the egg membrane, when it may be said to have hatched, but, unlike all other types of fish-embryos known to me, the young fish does not at once drop out of the egg-membrane when the latter is ruptured. This is prevented by the adhesion of the ventral (now upper) pole of the yolk-sack to the inside of the egg-membrane just before the latter is ruptured. Just how this secondary adhesion of the yolk-sack is effected has not been determined, but the adhesion persists until the embryos are considerably over one-half inch in length.

In the course of the development of other parts, the yolk-sack is finally constricted horizontally round the middle below the body of the embryo, and becomes hour-glass-shape. This is due in part to the down growth of the mesoblastic somites on either side of the yolk from above; as a result of this a part of the yolk becomes intra-abdominal while a part of it remains for a time in the lower bulb of the yolk-sack and outside of the true abdominal cavity. Eventually the whole of the yolk becomes intra-abdominal; this is due in part to its further absorption and the further development of the abdominal walls of the embryo, but during all of this time, or until yolk-absorption is completed, the embryo remains adherent as described above. At this stage the embryo is so far developed that it would be recognizable as belonging to the genus *Batrachus*.

The pectoral and pelvic fins develop as very short folds which are close together, the latter arising almost immediately behind the former. In the course of further development, the pelvic fins are suddenly translocated forwards in advance of the pectorals, and are finally brought to lie near the constriction in the yolk-sack and just above the lower bulbous portion of the latter. It will therefore be obvious to any one that neither the pectoral nor pelvic fins have anything to do with causing the adhesion of the embryos, for both of these fins arise far above the point where the young fish is adherent.

The paired spinal nerves which pass to the pelvic fins are caused to cross those passing to the pectorals, because of the sudden translocation of the former pair of fins already alluded to.

It has also been stated by authors that *Batrachius* possesses no lateral line. This is an error, for the writer found that the neuro-mastic grooves or furrows, which remain open for a considerable time on the heads of the larvae, are continued into a lateral line system on the sides, a condition of things which is also very evident in the adult, if the latter is carefully examined. There are also series of effluent pores present in the adults. The lateral neuro-mastic canal bifurcates in the vicinity of the shoulder-girdle and sends a dorsal branch backward below the base of the dorsal, and a ventral branch above the base of the anal. These two canals run nearly parallel along either side of the body and even extend backward upon the tail, as shown by some fine preparations of the skin of the embryo mounted by Professor Libbey, of Princeton.

Another point of some interest is the fact that the entire brood of young embryos upon any one stone have their heads directed one way and toward the light, which comes in at one side of the little retreat prepared by the adults. This is very remarkable and seems to indicate that the direction whence the light comes has some influence in determining the direction in which the embryonic axis will be formed in the blastoderm.

Very active movements of the tail, and especially of the pectoral fins, begin as soon as these parts are fairly developed; these movements become more energetic toward the close of the fixed stage of existence of the young toad fish. It is very probable that the active wriggling movements of the young embryos finally frees them from the surface to which they are firmly glued by some adhesive material secreted by the yolk-sack, but which, like that which in the first place caused the egg-membrane to adhere, is not soluble in water.

The yolk is peculiarly homogeneous and does not readily coagulate or harden in the presence of ordinary reagents, such as chromic acid, as long as the egg-membrane is intact. There are no oil-drops present and the ova are much heavier than their own volume of sea-water. The number of ova found in one brood varies considerably, but it does not seem that there are ordinarily much over two hundred laid in one place. They are dirty-yellow in color and very firm to the touch, with a very narrow space between the vitellus and enveloping egg-membrane.

The development of the toad-fish is peculiar, if not unique, in presenting a prolonged fixed stage after the period of hatching or escape from the egg-membrane is over, during which all or nearly all of the yolk is absorbed. The embryo is therefore finally set free, without being encumbered by a heavy yolk, such as is met with in the embryos of the salmon. Such a provision obviously has its advantages, especially since the young are also guarded by the male parent during the period of their helpless fixation. One

may frequently find recently hatched embryos, around the affixed pole of the yolk-sack of which shreds of the ruptured egg-membrane still adhere; during the later stages such shreds are not usually visible. There is a decidedly heterocercal tail developed from a special tail-fold, since there is no absolutely continuous median fin-fold developed, as in many other forms.

Oviposition occurs about the middle of July, in the latitude of Wood's Holl. How long it lasts has not been determined, but judging from the condition of the roes and milt of the adults at that time, it seems very probable that they do not spawn later.—

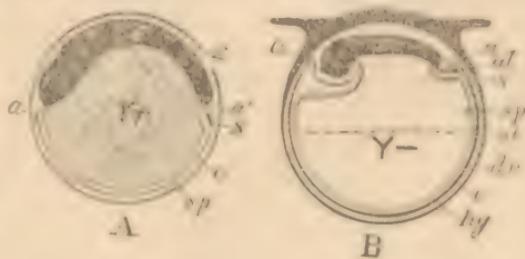
John A. Ryder.

(*American Naturalist Extra*, February, 1886.)

EMBRYOLOGY.¹

THE ORIGIN OF THE AMNION.—The purpose of the present note is to point out some of the mechanical conditions and causes which have been competent, in the course of the *development* of *development*, to bring about the formation of the amnion. No embryological writer, as far as I am aware, has ever attempted to trace the amnion to the part in the embryos of anamniated forms which led up to its development in the amniated ones. Balfour said, that "it does not seem possible to derive it from any pre-existing organ" (Comp. Embryol., II, 256). And he says further (op. cit., 257): "The main difficulty is the early development of the head-fold of the amnion." Balfour's view, that it is developed *pari passu* with the outgrowth of the allantois, is utterly inadequate to explain the genesis of the amnion of insects or that of *Peripatus edwardsii* and *P. torquatus*, for in them no allantois is formed. His hypothesis also breaks down in the light of the brilliant researches of Selenka on the inversion of the layers in the Rodentia.

A comparison of the longitudinal, vertical, diagrammatic sections, figures *A* and *B*, of an osseous fish-egg and a mammalian ovum respectively, will conclusively show that the somatopleure *s*, in *A*, is the exact homologue of the layer giving rise to the amniotic folds in *B*, though in *A* this layer merely covers the space



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between the yolk y and the somatopleure, leaving the coelomic space c , which has been derived directly in the osseous fish embryo from the cleavage cavity of the egg. We thus find that the preexisting structure, from which the amniotic folds are formed in the higher types, is already present in the embryos of osseous fishes. The next important point to demonstrate is, at what grade in the phylum of the Chordata traces of amniotic folds first appear, and whether such rudiments of an amnion are also found in the embryos of osseous fishes.

Glancing at A , it will be seen that there are rudimentary amniotic head and tail folds developed at a and a' , and that we, therefore, have traces of an amnion appearing for the first time in embryos of the grade of osseous fishes. This is not universal, however, for it is found that in species in which the zona radiata z does not closely invest the ovum, the embryo E is not pressed down into the vitellus, so as to raise the somatopleure s into a fold or duplication around the ends and along the sides of the embryo. The zona invests the ovum more or less closely in almost all Teleosts, but in a few, *Alosa*, for example, it does not, and in this species no traces of amniotic folds are ever developed.

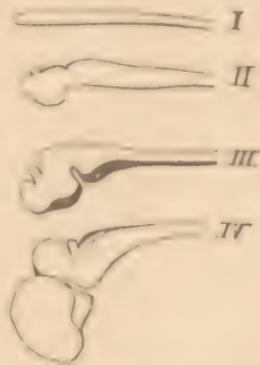
The embryo is differently conditioned in those eggs with the zona fitting closely around the ovum from those in which there is a great space around the egg, and between the latter and the zona. The inference, therefore, is that in the first case the embryo E is pressed down mechanically into the yolk by the presence externally of the rigid zona. As the embryo E grows, and the yolk substance of the ovum is converted into it, the latter is replaced in the space within the zona by the embryo. It is thus rendered evident, that, in those types of teleostean ova with a closely fitting zona, the rudimentary amniotic folds which are formed around the embryo have been mechanically caused by the rigid zona in the presence of the active forces of growth. If we examine the mechanical conditions under which the eggs of still higher forms are placed, we will find the same reasoning to hold. We are thus, it seems, obliged to conclude that the amnion in all forms has arisen in consequence of the forces of growth resident in the embryo, encountering peripheral and external resistance either in the form of a rigid outer egg-shell, zona radiata z , or decidua reflexa dr , or even the walls of the uterine cavity itself, supposing, of course, that a large vesicular blastoderm containing yolk has been formed by epiboly.

The gap between the truly epicyemate embryo, as seen in *Alosa*, and the endocyemate embryo of the *Paratheria* and *Eutheria* is, therefore, partly bridged by the presence of a rudimentary amnion, or amniotic folds in many teleostean embryos just prior to their escape from the eggs, or where the zona is ruptured. When this occurs the amniotic folds vanish, as in the embryos of many of the *Salmonidæ*, for example, and a closed amni-

otic sack is never formed, because, in the first place, the intra-oval period of development does not last long enough; nor, in the second place, is it possible, owing to the comparative small size of the yolk, and the rapid growth of the embryo, for the latter to become bodily invaginated into the blastodermic vesicle, which is filled with yolk. The amniotic folds can, therefore, not meet upon the middle line of the back, and coalesce, as they do in the higher endocytic forms. The development of a transient amniotic head-fold of greater width and in advance of the side and tail folds, is also prevented by the absence of a strongly marked cranial flexure in the embryos of Teleosts.

The mechanical effect of the gradual development of the cranial flexure in exaggerating the development of the amniotic head-fold in the Chordata, will be best appreciated by a glance at diagrams I, II, III, and IV, representing respectively the brain of an acraniate, a marsipobranch, an elasmobranch and a mammal. With the increase in the volume and area of the cerebral cortex, which occurs mainly on the dorsal and lateral aspects of the anterior end of the neurula, the acceleration of growth of the brain substance also occurs on those aspects, and a downward flexure of the floor of the brain necessarily takes place. The rapid enlargement of the cephalic end of the embryo of an endocytic, eutherian or paratherian form, and the rapid or precocious development of the cranial flexure, would naturally, in such a type, tend to cause the amniotic head fold to be developed earlier and to a greater extent than the tail-fold, as is shown in Fig. B, at a.

In the eutherian types, with inverted germinal layers, an amniotic head fold of the kind developed in normal forms is never formed, because the cavity of the true amnion in the former is developed by the vacuolization or the formation of a cavity or cavities in the solid epiblastic mass, and not by invagination. In the Trachitae possessing an amnion there is no cephalic flexure, and the part of the amnion which is first developed in the most pronounced manner is often the tail fold, due apparently to the ingrowth of the caudal end of the embryo into an involution of the blastoderm, confined in a rigid egg-envelope, the involution being thrust into the yolk. Later, with the growth and encroachment of the head-end of the embryo upon the yolk, the abdomen is again everted in some cases from its amniotic sack. In *Periatus eucardia*, according to Von Koenig, cleavage is total, the development is viviparous and intra-uterine, a hollow blastula is formed, the embryonic area at one pole of the blastula is invaginated into the latter, so that the ventral surface of the embryo is



directed towards the roof of the amniotic cavity, the reverse of the eutherian embryo. An umbilical stalk is also formed, which springs from the dorsal surface of the embryo and passes to a partially zonary placenta, disposed in relation to the uterine walls in exactly the same way as that seen in the embryo of Carnivora. If we now regard the dorsal surface of the embryo of *Peripatus edwardsii* as homologous with the ventral surface of the embryos of Carnivora, the resemblance between the modes of development of these two types becomes still more startling. While it is manifestly absurd to even attempt to suppose, on the strength of these resemblances, that there could be any genetic affiliation between the Carnivora and Malacopoda, the only way out of the difficulty seems to be to suppose that the similar methods of development of the two arose in response to the similar conditions which environ the ovum during its early stages of growth.

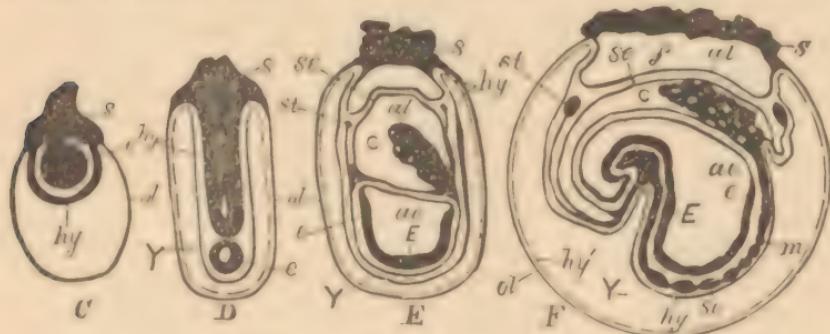
The differences between Von Kennel and Sedgwick, as to the modes of development of *P. edwardsii* and *P. capensis*, it seems to me, may be readily understood and reconciled when it is considered that the first is holoblastic and endocytic, while in the latter the egg is meroblastic, and apparently undergoes an epicyclic process of development.

All the data in the foregoing paragraphs unequivocally support the thesis that the amnion has been developed mainly by mechanical means and conditions.

The rigid zona of the epicyclic teleostean embryo, as shown in Fig. *A*, in which the yolk *y* is a positive quantity, is represented by the maternal envelope *dr* in Fig. *B*, in which the yolk, as such, is absent. The gap between the condition of *A* and that of the types with apparently inverted germinal layers, so completely elucidated by Selenka, is a wide one; yet it seems easy to pass from the primitive condition of *A* to that of the extremest form, viz., the guinea-pig; if the rabbit, mole (Heape), the vole (Kupffer), and the mouse and rat (Selenka), are considered as intermediary steps. So complete or extreme has been the invagination of the embryonic mass or area in these forms that, in the extremest type, the embryo is finally developed at that side or pole of the primitive blastula which is exactly opposite the point where the blastodisk was originally formed, as in normal Eutheria. The way in which this is accomplished is quite remarkable, and may now be described, as the process is a special modification of that by means of which the usual endocytic condition is brought about.

Selenka finds that there is an outer layer of cells, *ol*, Fig. *C*, split off from the ectoblast, as first described by Rauber, in the rabbit's ovum, and which take no direct part in the formation of the embryo. He also finds that upon the further growth of the ovum, after the blastula stage is reached and the germinal area or disk is developed, the blastula rapidly elongates in the direc-

tion of the diameter extending from the centre of the blastodisk to the opposite pole. By this time the blastula has become



adherent to the uterine epithelium through the intermediation of the transitory outer layer of cells, *ot* (*Reichert'sche Deckschicht*), already mentioned, but the constituent cells of a certain portion of this outer layer, just overlying the germinal disk, as indicated at *s*, rapidly proliferate, so as to form a lenticular or columnar thickening or mass, constituting what Selenka calls the *Träger*, a term which may be anglicized by the word *suspensor*. This suspensor immediately overlies and pushes the germinal area, or mass inwards before it, down into the hollow cavity of the blastula. The germinal area is either pressed inwards into the hollow blastula, so that it assumes a concave form above, with a cavity between it and the lower surface of the suspensor, as in *Arvicola*, or the epiblast forms a solid mass, before which the hypoblast is pushed inwards by the ingrowth of the suspensor, so that the blastula assumes the form of an elongated sack, as in the ovum of the rat or the guinea-pig.

The process just described is somewhat similar to that of gastrulation, for the germinal pole of the blastula is pushed downward into the sack formed by the hypoblast and outer layer, so that the embryo is finally developed quite at the opposite pole of the elongated blastula, as in the guinea-pig. The steps by which the mode of development of the embryo of the latter came to be established will be much better understood by reference to diagrams *C*, *D*, *E*, and *F*, representing four stages of the development of the rat copied from Selenka.¹ In these figures it will be obvious to the reader that the principal result of the precocious invagination of the embryonic area is to throw the embryo to the opposite pole of the egg, and to so encroach upon the cavity of the mesenteron, the umbilical vesicle, as to almost obliterate it, as is shown in Fig. *F*. The embryo *E* is also bent into a curve, just the reverse of that shown in Fig. *B*. The coelomic space *c* is also more restricted, and the sinus terminalis *st*, in Fig. *F*, seems to

¹ Studien über Entwickelungsgeschichte der Thiere. Drittes Heft. Die Blätter umkehrung im Ei der Nagethiere, 4to. Wiesbaden, Kreidels, 1884.

terminate towards the dorsal pole of the ovum instead of the ventral, as in Fig. *B*.

In the ovum of the guinea-pig the obliteration of the umbilical vesicle *y* is carried still farther than in Fig. *F*, because the hypoblastic layer *hy'*, next to the layer *ol*, is absent, and the hypoblast lying just under the embryo is brought into immediate contact with the layer *ol*, thus giving rise to the illusion that a complete inversion of the primary embryonic layers has occurred. I say illusion, because there has been no actual inversion of the primary layers, for the latter have been merely shoved to the opposite pole of the eggs into contact with the layer *ol*, where embryonic development has proceeded in the normal way, being modified only by the displacement which the germinal area has suffered in relation to the other essential parts of the ovum. It is as if the germinal pole of the blastodermic vesicle had become concave instead of convex, and collapsed inwards against the inside of its lower pole, the walls of which consist of the hypoblast of the inferior pole of the umbilical vesicle—mesenteron, and the outer layer.

The difficulties which Balfour speaks of have, I hope, been satisfactorily cleared away by what has been said above, and a rational and connected hypothesis as to the genesis of the amnion firmly established. I am aware that many objections may be urged against the views here propounded, but I cannot think that any other view of the case will so satisfactorily reconcile and coördinate the facts involved. To those who take a philosophical view of such subjects, it will be obvious that the deductions here reached give but little countenance to the idea that amniotic characters can be always profitably used in taxonomy, at least, not until the forces which have led to their development are better understood. On the theory of the development of development, the extreme modification of the amnion of some of the Rodentia would cause the latter to take higher rank than the Primates, because, as shown in Fig. *F*, the primary amniotic cavity becomes divided, and a relatively large false amniotic cavity *f* remains just under the suspensor *s*, and shut off from the true amniotic cavity *ac* by the intervening serous envelope *sc*, the cœlomic space *c*, and the somatopleural root of *ac*. Such a casing, however, is obviously not legitimate in the light of the above mechanical hypothesis of the genesis of the amnion.

To briefly summarize, we find that the first traces of amniotic folds met with in the embryos of the lower types of Chordata are caused by the resistance from without offered to the growth of the embryo by a rigid zona radiata. In such types the amniotic folds are transitory, and disappear at the time the zona is ruptured. After a larger yolk has been acquired the embryo undergoes a longer period of intra-oval development, so that the period of the persistence of the amniotic folds, produced as before, is prolonged.

With the increase in the size of the embryo, in these large-yolked forms, it is finally thrust down into a saccular involution of the blastoderm, the lips of the opening of which meet over the back of the embryo where they coalesce, the outer limb of the duplication giving rise eventually to the serous envelope, and the inner to the roof of the amniotic cavity. In those types which have the primary layers apparently inverted, the rapid ingrowth of the suspensor precociously invaginates the germinal area inwards before the embryo is distinctly developed, so that it is not formed in its usual or normal position. These extreme modifications were not possible until after the loss of the food-yolk, after which a hollow blastodermic vesicle still continued to develop, filled with a thin albuminous or serous fluid instead of a dense yolk material. The tendency of the eutherian ovum to form a large, hollow blastodermic vesicle or blastula is doubtless an inheritance transmitted from a paratherian source. The bodily invagination of the whole embryo and the more or less complete obliteration of the cavity of the umbilical vesicle by the rapid growth of the enlarging amnion, would be readily accomplished in the course of the development of the eutherian ovum.

EXPLANATIONS OF THE REFERENCE LETTERS USED IN THE FIGURES.

a amniotic head-fold, *a'* tail-fold, *ac* amniotic cavity, *al* allantois, *c* coelomic space or continuation of body cavity, *dr* decidua reflexa of uterus, *E* embryo, *e* epiblast, *f* cavity of false amnion (*falsche Amnionhöhle*), *hy* hypoblast, *hy'* hypoblastic outer wall of umbilical vesicle, *m* mesoblast, *ol* outer layer (*Reichert'sche Deckzellen, Deckschicht*), *s* suspensor (*Tiäger*), *se* serous envelope, *so* muscular somites, *sp* splanchnopleure (= the periblast in Fig. A), *st* sinus terminalis, *Y* yolk, with + and — signs to indicate its presence or absence.

—John A. Ryder.

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